The latest Ordovician Hirnantian brachiopod faunas: New global insights

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ABSTRACT

The temporal and spatial distribution of Hirnantian brachiopod faunas are reviewed based on a new, comprehensive dataset from over 20 palaeoplates and terranes, a revised correlation scheme for Hirnantian strata and numerical methods including network analysis. There were two successive evolutionary faunas: 1. the widespread and diachronous *Hirnantia* Fauna related to the glacial acme in the early–mid Hirnantian, including shallow, deeper and deep-water communities that diversified in much more complicated environmental conditions than hitherto envisaged; and 2. the Edgewood-Cathay Fauna (new term) thrived during post-glacial, warmer, shallow-water regimes with both carbonate and siliciclastic facies from low latitudes in the late Hirnantian–early Rhuddanian. The two survival faunas can occur in the same order in different regions, immediately following the first and second phases of the Hirnantian crisis, respectively. This faunal succession records two climatic perturbations, one with a glaciation, associated with climatic cooling and a global low-stand, during which the *Hirnantia* Fauna flourished, and a second characterized by melting ice, global warming, and

sea-level rise (with global anoxia), aligned to the development of the Edgewood-Cathay Fauna and the repopulation of the seas by many animals adapted to warmer water, e.g., metazoan reefs, massive tabulates, and sponges. Changes in many properties of the *Hirnantia* Fauna may have resulted from the heterogeneity of global climate change in time and space; contrasts in the Edgewood-Cathay faunas record differences between carbonate and siliciclastic deposition, respectively, at low latitudes. Intense climate changes, sea-level fluctuations, and oceanographic ventilation and anoxia, had important roles in brachiopod evolution through the Hirnantian extinctions as first taxa confined to warm-water and then cool-water conditions were the main victims. During the Hirnantian, higher originations of new taxa may have been a response to crises, which increased the rate of phyletic evolution due to extreme climatic conditions.

Keywords: Hirnantian crisis; Gondwanan glaciation; Brachiopod evolution; *Hirnantia* Fauna; Edgewood-Cathay Fauna; Environmental complexity and perturbations.

1. Introduction and global context

The end-Ordovician mass extinction is the first of the major Phanerozoic extinction events, linked to the waxing and waning of a major glaciation and associated habitat destruction, in both shallow and deep water. The *Hirnantia* brachiopod fauna, is one of the most distinctive, globally-distributed (e.g., Temple, 1965; Rong and Harper, 1988; Sheehan, 2001; Rasmussen, 2014) and short-lived (cf. Brenchley *et al.*, 1994; Armstrong, 1995; Ling *et al.*, 2019) marine faunas. It is regarded as a major indicator of crisis in a unique ecosystem where the fauna was differentiated into a series of

communities across latitudes, water depths, and lithologies. Its origin and demise were related to the first and second strikes of the abrupt, end-Ordovician mass extinction. Interrogation of global databases has indicated that the extinctions occurred earlier than the Hirnantian (e.g., Rasmussen *et al.*, 2019). Our data relates specifically to brachiopod distributions during the Hirnantian based on the examination by the authors of sufficiently documented sections and their faunas through the uppermost Katian to lower Rhuddanian. There remain, however, questions around what is a very substantial series of faunal turnovers at the end Ordovician, where did the Lazarus taxa hide, and what were the causes and consequences of this significant, global event?

The *Hirnantia* Fauna has been a key focus for over half a century since the seminal work by Temple (1965). It highlights biotic and environmental changes during the crisis and its distribution has been critical in correlating and defining the Ordovician–Silurian boundary. Since Rong and Harper (1988), a substantial number of papers related to the Fauna have provided much new information, increased biostratigraphic precision and improved taxonomic revisions of the Fauna. The rarefaction curve based on the data from extensively sampled sections on the South China Palaeoplate reveals that a plateau has already been reached with about 28 genera and nearly 100 occurrences of the fauna (Harper and Rong, 2008). Meanwhile, data from the Kosov Formation in Bohemia, reporting 25 taxa suggest a similar high diversity for the fauna (Havlíček, 1990; Mergl, 2011). It is noted that the term "diversity" used in this paper refers to numbers of genera (richness) in the Hirnantian faunas, a related community, assemblage, or sample, and not in the sense (richness+abundance) strictly applied by biologists.

New studies on the fauna from Estonia–Latvia (Hints, 2012; Hints *et al.*, 2012, 2016; Hints and Harper, 2015; Harper and Hints, 2016), Sweden (Dahlqvist *et al.*, 2010), Denmark (Harper and Nielsen,

2015), Norway (Bockelie *et al.*, 2017), England (Brenchley *et al.*, 2006), European peri–Gondwana (Villas *et al.*, 1999; Leone *et al.*, 1991; Álvaro *et al.*, 2016; Bernárdez *et al.*, 2014; Colmenar *et al.*, 2018, 2019), North Africa (Sutcliffe *et al.*, 2001; Villas *et al.*, 2006, 2016; Colmenar and Álvaro, 2015; Colmenar *et al.*, 2018), western Argentina (Benedetto, 2003; Leone and Benedetto, 2019), Sibumasu (Cocks and Fortey, 1997, 2002; Rong *et al.*, 2020; Huang *et al.*, 2020a), New Zealand (Cocks and Cooper, 2004), Bolivia and Paraguay, South America (Benedetto *et al.*, 1992, 2013) have afforded new data for a better understanding of the nature of the *Hirnantia* Fauna in both high and low latitude regions.

New and existing data demonstrate that there were two successive brachiopod faunas within the Hirnantian: the *Hirnantia* Fauna in early–middle Hirnantian, and the succeeding Edgewood-Cathay Fauna in late Hirnantian to Rhuddanian. The latter is known to contain two facies: carbonate facies with the previously named Edgewood Fauna, typically developed in the Mid Continent, USA (Amsden, 1974), and the siliciclastic facies, exemplified by the Cathay Fauna in South China (Rong *et al.*, 2013). This brachiopod succession reflects two climatic perturbations, one with a glaciation, associated with climatic cooling and a global low-stand, during which the *Hirnantia* Fauna flourished, and another characterized by melting ice, global warming, and sea-level rise, aligned with the development of the Edgewood-Cathay Fauna.

Our comprehensive revision of late Ordovician and earliest Silurian brachiopod faunas brings into focus a number of key questions, some with relevance to other Phanerozoic extinctions. This paper provides: 1. New data pertinent to a better understanding of the origin, evolution and extinction of many taxa in the *Hirnantia* Fauna and the succeeding Edgewood-Cathay Fauna; 2. Improved knowledge of temporal and spatial variation of common taxa in the two faunas; 3. New information on

their distribution that is helpful in evaluating biogeographical endemism and the location of species pumps during the terminal Ordovician; 4. New bases for further analyses on the significance of the two successive faunas in a global context; 5. New insights on the macroevolution of brachiopod faunas through the Ordovician and Silurian transition.

2. Methodology

We present here a new database based on primary capture from the literature (and our own regional databases) with where possible an assessment by the authors of the quality of fossil identifications and stratigraphical control. This review is conducted mainly at the higher taxonomic levels (genus to order) recorded in the *Hirnantia* Fauna and Edgewood-Cathay Fauna. Those indeterminate taxa at generic level are not included in the new databases, and the rare families, or superfamilies recorded from the literature are omitted if no generic representatives were identified. Species are critically important, but require a substantial amount of additional systematic work. Our investigation shows that there are a considerable number of the most common genera of the faunas possess an excessive number of species. As an extraordinary example, *Eostropheodonta* involves more than 20 nominal and undetermined species in the Hirnantian (Rong and Cocks, 1994); many characters highly vary within a population, and are explained as intraspecific variations rather than by specific discrimination (Rong *et al.*, 2020; Huang *et al*., 2020b). Larger samples of many taxa, now available from a range of localities, reveal that many species may represent a continuum of geographic variation and this may contribute to our review of the nature of the end Ordovician crises.

The most intensive investigations of the *Hirnantia* Fauna are documented from South China and a

global correlation of Hirnantian rocks is presented, based on these sections as a standard, to unravel the complex dynamics of the *Hirnantia* Fauna. The assertion that the *Hirnantia* Fauna–bearing beds are diachronous (Rong *et al.*, 2002) is further confirmed by new data provided herein, and for the great majority, occurrences are within the lower–middle Hirnantian Stage, indicating a cool/cold-water environment during the Gondwanan glaciation. An informal vertical partition of the Hirnantian Stage into three parts (e.g., Rasmussen and Harper, 2011b) is accepted herein based on data collected from a number of studies (graptolites, e.g., Koren *et al*., 2003; Chen *et al*., 2006; Melchin *et al*., 2013; Štorch *et al*., 2018) and our investigation. It includes lower (=lower–middle *Metabolograptus extraordinarius* Biozone), middle (=upper *M. extraordinarius* to lower *M. persculptus* biozones), and upper (=upper *M. persculptus* Biozone) Hirnantian.

The recognition of a new biogeographic unit, the Edgewood-Cathay Fauna requires a new database to capture additional information from, for example, Laurentia, Baltica, Kolyma, Gornyi Altai, South China and Zeravshano-Gissar Mountains distributed on eight palaeoplates or terranes, all from low latitudes.

The dataset on the two faunas, and their communities or associations was compiled through examination of original specimens, related collections, and the literature. Every attempt has been made to ensure that all the genera of the two faunas have been accounted for, and the composition, and origin of both faunas are analyzed for the first time. Although taxonomic knowledge of the *Hirnantia* Fauna is more comprehensive than that for the Edgewood-Cathay Fauna, this new, expanded dataset remains a reliable resource to reflect a global scenario for the evolution of the brachiopods through the Ordovician and Silurian interface.

In this study, network analysis (NA) is employed to investigate the geographical distribution of the Hirnantian brachiopod faunas. NA has been used in biogeographic studies (e.g., Sidor *et al.*, 2013; Vilhena and Antonelli, 2015) and has been successfully applied to palaeobiogeographical studies (e.g., Kiel, 2017; Huang *et al.*, 2016, 2018). Compared with other commonly adopted methods in palaeobiology (e.g., CA and PCA), NA provides a network diagram, displaying more information about structure of the dataset. The method is able to show how a locality (a collection) is linked to others via the taxa they share, by which the distributional patterns of the Hirnantian brachiopod faunas can be visualized. More importantly, distribution of the brachiopod genera across regions and the relationships among and between different faunas can be illustrated.

3. Reappraisal of the *Hirnantia* Fauna

Our new dataset includes a large number of occurrences of the various associations or communities assigned to the *Hirnantia* Fauna from all over the world (Appendix I-A). These occurrences are assigned to over 20 palaeoplates or terranes based on Torsvik and Cocks (2017) (Fig. 1). They include North Africa (Algeria, Libya, and Morocco), Ala Shan (western Inner Mongolia, China), Avalonia (England, eastern Ireland, and Wales), Baltica (Denmark, Estonia, Latvia, Norway, Poland, and Sweden), European peri–Gondwana (Austria, France, Italy, Portugal, and Spain), Kazakh Terranes (Chu–Ili), Laurentia (Québec), Lhasa (central Xizang, China), Marginal Laurentia (Maine and Scotland), New Zealand, Perunica (Bohemia, Czech Republic), Precordillera (San Juan, Northwest Argentina), northern Qilian (Gansu, Northwest China), Sibumasu (Myanmar, Thailand, and western Yunnan, China), South China (northeastern Yunnan, Guizhou, Sichuan, Shaanxi, Chongqing, Hubei,

Hunan, Jiangxi, Anhui, Jiangsu, and Zhejiang), and the Continent of South America (Bolivia and Paraguay). All the relevant references are cited in subsequent sections. The data from Ala Shan, New Zealand, and Qilian, although not conclusive, are still included in our basic dataset (Appendix I-A).

The records of the so-called *Hirnantia* Fauna from Tasmania of Australia, Gornyi Altai, Turkey, South Africa, Chingiz of Kazakh Terranes and others are considered to be doubtful and are provisionally excluded from the new database for the *Hirnantia* Fauna (see discussion below).

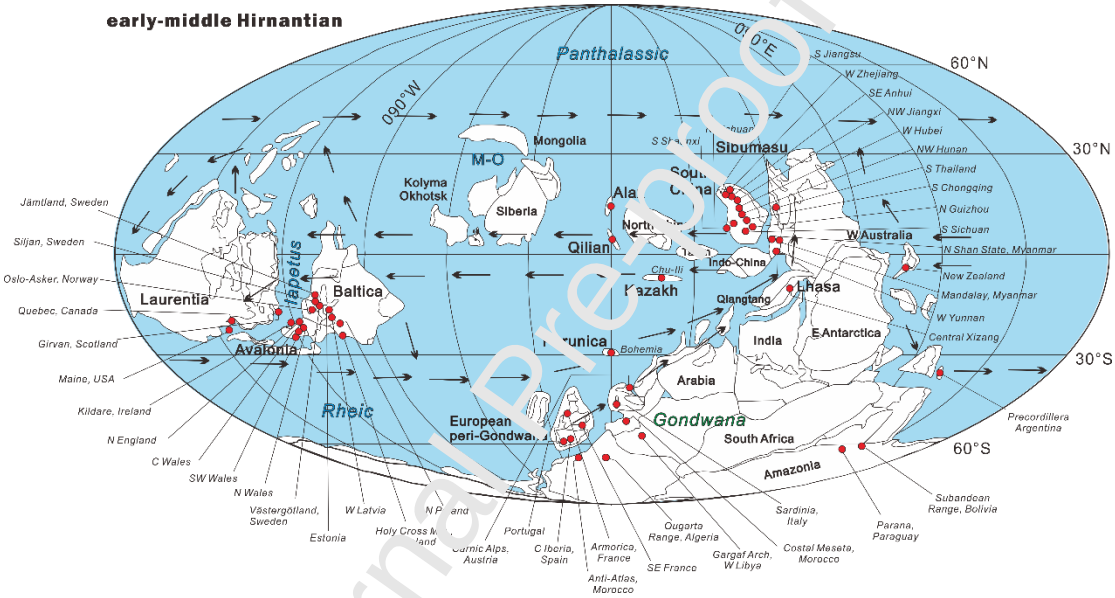

Fig. 1. Global occurrences (red circles) of the *Hirnantia* brachiopod Fauna in the early–middle Hirnantian based on the global reconstruction of Torsvik and Cocks (2017).

3.1 New dataset for the Hirnantia *Fauna*

3.1.1 North Africa

An atypical *Hirnantia* Fauna has been reported in the Hirnantian rocks of Morocco, Algeria, and Libya (Havlíček, 1971; Havlíček and Massa, 1973; Mergl, 1983; Havlíček, 1990; Sutcliffe *et al.*, 2001). A synthesis of the Fauna in the Bani Province was provided by Sutcliffe *et al.* (2001). They noted that

the presence of *Hirnantia* and *Eostropheodonta* associated with *Arenorthis* and *Destombesium* in the Lower Second Bani Group marks the first step in the colonization of the fauna during the initial growth of the Hirnantian ice sheet. Later, a similar assemblage was recovered from the glacio-marine facies of the Tamekhart Member in the Upper Second Bani Group, eastern Anti-Atlas, Morocco, suggesting adaptation to peak glacial conditions (Villas *et al.*, 2006). Moreover, *Kinnella* and *Plectothyrella* were reported from the upper Lower Second Bani Formation in central Anti-Atlas (Villas *et al.*, 2016). This indicates that *Kinnella* invaded cold-water regimes during the early–middle Hirnantian. Recently, *Clarkeia*, *Dalejina* and some undeterminate taxa were reported from the Lower Second Bani Group and *Hirnantia*, *Destombesium*, *Eostropheodonta*, *Arenorthis*, *Kinnella* and *Plectothyrella* from the Upper Second Bani Group (Colmenar and Álvaro, 2015; Colmenar *et al.*, 2018). In addition to Mergl (1983), a low-diversity *Hirnantia* Fauna, including *Hirnantia*, *Plectothyrella*, *Libyaeglossa*? and *Leptaena*?, is recorded from the Ougarta Ksar Member of the Djebel Serraf Formation, Algeria (Popov *et al.*, 2019).

3.1.2 Alax

This is a part of the Alxa Shan Terrane and may have been located in the tropical area of the northern hemisphere, possibly close to the North China Palaeoplate in the Early Palaeozoic (Xiao *et al.*, 2009; Torsvik and Cocks, 2017). A sample of shelly fossils was collected from grey bioclastic limestone (60–70 cm thick) in the Danmianshan Bed, 135 km east of Ejin Banner town, western Inner Mongolia (Rong *et al.*, 2003). The brachiopods include *Cliftonia*, *Dalmanella*, *Leptaena*, *Triplesia* and associated with the trilobites *Mucronaspis*, *Decoroproetus*, *Niuchangella* and *Solariproetus* (Qu, 1986). This bed is underlain by the Badanjilin Formation (upper Katian) yielding *Holorhynchus*, and is

overlain by the basal Guaizihu Formation (upper Hirnantian), from which graptolites of the *Akidograptus ascensus* Biozone were recovered at a level 1.87 m above the Danmianshan Bed.

3.1.3 Avalonia

The typical *Hirnantia* Fauna occurs in Wales, England, and Ireland. The brachiopods from the Wenallt Formation in the Garth area, Central Wales (Williams and Wright, 1981) are excluded from our database based on the reasons noted below.

3.1.3.1 Keisley, England A reappraisal of the Keisley Fauna from rocks above the Keisley Limestone at Keisley, Cumbria, England (Temple, 1968; Wright, 1995; Cocks, 2008) indicates that 1. The percentage of characteristic taxa of the *Hirnantia* Fauna in the collection is low; e.g., *Hirnantia* (0.05% of the entire brachiopod fauna), *Kinnella* (0.1%), *Hindella* and *Draborthis* (each 0.6%), and *Paromalomena* (2.1%); 2. *Leptaena*, *Eostropheodonta*, *Dalmanella*, *Cliftonia*, and *Plectothyrella* are absent; 3. Most abundant are the craniids *Xenocrania* and *Petrocrania* accounting for 41.1%; 4. The richest taxon is *Skenidioides* (16.8%); 5. Most common among the orthides are *Toxorthis* (7.9%) and *Dolerorthis* (6.2%). This high-diversity association is loosely related to the *Hirnantia* Fauna. On the presence of deep-water elements, like *Skenidioides*, *Dicoelosia*, and *Templeella* (=*Kayserella*? of Temple, 1968), and the overwhelmingly small sized individuals, the Keisley Fauna may have inhabited deep-water environments (BA4) during the early–middle Hirnantian, as a variant of the *Hirnantia* Fauna.

3.1.3.2 Meifod, Central Wales Siliciclastic facies capping karstified limestones at Meifod, Wales

(Brenchley *et al.*, 2006) contain a brachiopod assemblage dominated by *Hindella* together with *Hirnantia*, *Kinnella*, and *Plectothyrella* from the Craig-wen Sandstone. It is more likely that the sandstone is of early–middle Hirnantian age rather than late Hirnantian (Schmitz and Bergström, 2007) because of the presence of the typical *Hirnantia* Fauna.

3.1.3.3 Yewdale Beck, England A small brachiopod fauna, in Yewdale Beck, English Lake District, is dominated by the species of *Hindella*, *Kinnella*, *Mirorthis*, *Paromalorthis*? and *Plectothyrella*, and is interbedded with a graptolite fauna including *Akidograptus ascensus*, *Atavograptus ceryx*, *Metabolograptus parvulus* and *Normalograptus* spp. within the lower Skelgill Formation (Harper and Williams, 2002). Based on the presence of some characteristic elements of the *Hirnantia* Fauna, these brachiopods were assigned to the Fauna (Harper and Williams, 2002). They may represent the youngest documented occurrence of the Fauna. The specimens are small but mature individuals, presumably representing a relic fauna seeking refuge in less well-oxygenated, deep-water environments of the Cumbrian basin.

3.1.3.4 Kildare, Ireland Wright (1968) documented in detail a *Hirnantia* Fauna from the Chair of Kildare in the Leinster Terrane, marginal to, or a part of Avalonia. *Cliftonia* (37%) and *Hindella* (=*Cryptothyrella*, 35%) were recorded as most common taxa identified by Wright (1968) and Cocks and Price (1975), respectively. They are associated with *Dalmanella*, *Hirnantia*, *Leptaena* and *Plectothyrella*, ranging in abundance from 12% to less than 1%. The relatively low diversity *Hirnantia* Fauna may have lived in a shallow water setting.

3.1.4 Baltica

3.1.4.1 Sweden Through the detailed systematic work of Bergström (1968), a typical, relatively high diversity *Hirnantia* Fauna was described from the Loka Formation, Västergötland. The Hirnantian shelly faunas reported from five localities in Jämtland, were investigated by Dahlqvist *et al.* (2010). They recognized a clear depth zonation with 1. Shallow-water, near-shore facies dominated by rhynchonellides, 2. Shallow to mid-shelf depths by *Eostropheodonta*, *Hindella* and *Hirnantia*, and 3. Deep-water facies, mainly siliciclastics, by *Aegiromena* and *Paromalomena*. Similar patterns of brachiopod distribution have been also documented from South China (Rong *et al.*, 2018).

3.1.4.2 Norway Stratigraphically, the uppermost Ordovician in the Central Oslo region, Norway is complicated (Brenchley and Cocks, 1982; Bockelie *et al.*, 2017). There are two sets of brachiopod associations belonging to the *Hirnantia* Fauna and the succeeding Edgewood Fauna from the Hirnantian rocks (Cocks, 1982), which agrees with the preliminary conclusion of Rong and Harper (1988). The *Hirnantia* Fauna is exemplified by the *Hirnantia* Association from the basal parts of the Langøyene and Langära formations (Cocks, 1982). Although along with *Mucronaspis mucronata*, the assignment of the *Hindella-Cliftonia* Association from Langåra W17 (localities 9 and 33) and Kunglugen E16 (30), Asker, and the *Dalmanella* Association from Husbergøya three, Oslo and Høyerholmen 14, Asker remains inconclusive, they may presumably represent a low-diversity *Hirnantia* Fauna, as those encountered in northwestern Guizhou.

3.1.4.3 Estonia–Latvia Recently, new and existing data on the *Hirnantia* Fauna of Estonia–Latvia have been published and reviewed. The most diverse collections occur in west Latvia with a typical

Hirnantia Fauna in the Kuldiga Formation (Hints and Harper, 2003; Hints *et al.*, 2012; Hints and Harper, 2015; Harper and Hints, 2016). There are about 20 genera with *Dalmanella* being most abundant (37% of the whole). The next richest taxa, in decreasing order of abundance, are *Eostropheodonta*, *Cliftonia*, *Hindella* and *Plectothyrella*, along with *Hirnantia*, *Kinnella*, *Draborthis*, *Paromalomena*, *Leptaena*, and *Fardenia.* Harper and Hints (2016) provided a summary and analysis of the *Hirnantia* Fauna across the Baltoscandian Region and pointed out that there occur two fundamentally different Hirnantian brachiopod faunas in that region, the typical *Hirnantia* Fauna characteristic of the Kosov Province in the Kuldiga Formation and its corresponding units, and the Edgewood Fauna associated with Bahamitic type oolitic carbonates in the Saldus Formation and its coeval strata.

3.1.4.4 Denmark A deep-water *Foliomena* brachiopod association was recorded from the upper Katian Lindegård Mudstone of Bornholm, Denmark (Harper and Nielsen, 2015). The deep-water facies persisted into Hirnantian on Bornholm where the shelly fauna is characterized by sparse *Aegiromena*, indicating a deep-water association of the *Hirnantia* Fauna. The latter is essentially similar to that of South China during the terminal Ordovician crisis.

3.1.4.5 Poland The *Hirnantia* Fauna in Holy Cross Mountains, Southern Poland was recorded as typical, moderately diverse, having ten genera. Noticeably, *Kinnella* is the most abundant genus, occupying about 50% of the whole fauna in quantity (Temple, 1965); the two common genera are *Dalmanella* and *Hirnantia*, along with *Eostropheodonta*, *Paromalomena*, *Plectothyrella*, *Mirorthis*, and others. Unusually, *Xenocrania* (=his *Philhedra*?), a rare element elsewhere, appeared fairly common

(about 7% of the whole brachiopod fauna) in this region.

3.1.5 European peri–Gondwana

In the last two decades, research on the *Hirnantia* Fauna in the northern margin areas of Gondwana, i.e., France, Spain, Portugal, Carnic Alps, and Sardinia of Italy has advanced considerably providing a fairly clear picture of the shelly fauna in this region.

3.1.5.1 Portugal and Spain Young (1990) and Brenchley *et al.* (1991) reported *Paromalomena* and *Plectothyrella* from the phase 5 (Hirnantian) of Central Portugal, indicating the presence of a low diversity *Hirnantia* Fauna in this region. Colmenar *et al.* (2019) recorded *Paromalomena*, *Mirorthis*, *Plectoglossa*, and *Plectothyrella*, associated with *Mucronaspis mucronata* from the Ribeira de Braçal Formation (Hirnantian) of Central Portugal.

A low-diversity *Hirnantia* Fauna including *Hirnantia* and *Plectothyrella* was first documented from the Criadero Quartzite of Almaden in the Central Iberian Zone in south–central Spain (Villas *et al.*, 1999), and *Kinnella* was reported later (Bernárdez *et al.*, 2014).

In the Cantabrian Zone of Northwest Spain, there occur new Hirnantian assemblages: 1. A low diversity one including *Arenorthis*, *Eostropheodonta* and *Plectothyrella* at Valdeteja; 2. A higher diversity one containing *Eostropheodonta*, *Leptaena*, *Hirnantia*, *Draborthis* (=their Cremnorthidae gen. nov.), *Cliftonia*, *Orbiculoidea*, *Plectothyrella*, and *Hindella* at Argovejo (Bernárdez *et al.*, 2014). Interestingly, there co-occurs a typical *Hirnantia* Fauna and *Arenorthis*, a typical element of the Bani Province, in the same region, presumably indicating a link of this region with the Kosov Province.

3.1.5.2 Carnic Alps A low-diversity *Hirnantia* Fauna was recorded by Jaeger *et al.* (1975). The palaeontology and stratigraphy of the Ordovician–Silurian boundary rocks have been further investigated by Schönlaub *et al.* (2011).

3.1.5.3 Sardinia A *Hirnantia* Fauna of low diversity including *Hirnantia*, *Kinnella*, *Dalmanella*, *Mirorthis* and *Plectothyrella* was recorded from the Serra Corroga Member (Hirnantian) in Sardinia (Leone *et al.*, 1991). The presence of several typical elements of the Fauna suggests that the assignment of this location to the Kosov Province is appropriate.

3.1.5.4 France Several brachiopod assemblages associated with lower Hirnantian marine glacio-marine deposits, predating the peak of sea-level fall were reported from France. Mélou (1987) first recorded a low diversity assemblage (*Hirnantia* and *Plectothyrella*?) from the Armorican Massif. Álvaro *et al.* (2016) described five shelly associations as representatives of the *Hirnantia* Fauna from the Marmairane Formation (Hirnantian) of the Mounhoumet massifs, Southern France. Among them, the Association 5 has a relatively higher diversity with abundant *Kinnella*, associated with *Hirnantia*, *Eostropheodonta*, *Leptaena*, *Dalmanella*, *Plectothyrella*, *Hindella*, *Leangella* and others. Although the others possess a lower diversity (e.g., *Plectothyrella*, *Eostropheodonta*, and *Hindella*), their assignment to the *Hirnantia* Fauna cannot be excluded.

3.1.6 Kazakh Terranes

The Hirnantian assemblages have been reported from Chu–Ili (Nikitin *et al.*, 1980) and Chingiz–Tarbagatai (Popov and Cocks, 2014, 2017). Chu–Ili contains a distinctive representative of the

Hirnantia Fauna with a moderate diversity, whereas the assignment of the assemblage from Chingiz–Tarbagatai remains unresolved. There are more than three sites known in Chu–Ili that contain the fauna in the Zhalair Formation. In the Ojsu Creek (Number 286), an association is characterized by *Dalmanella*, *Cliftonia*, *Leptaena*, *Fardenia*, *Templeella* (=their Enteletacea gen. *et* sp. indet., pl. 10, figs 13–15 of Nikitin *et al.*, 1980) and others, and by lacking *Hirnantia*, *Paromalomena*, *Plectothyrella* and *Hindella*. In the Aschisu Anticline, Krylo north, the Durben collection (287 and 94) shows that in addition to the key taxa (e.g., *Hirnantia*, *Paromalomena*), there occur *Anisopleurella* and *Aegiromena*, as a distinctive feature of this fauna there, suggesting a closer relationship with the *Hirnantia* Fauna of western Yunnan (Huang *et al.*, 2020a, c). The material from the Zhideli area (264) yields only *Paromalomena*, possibly indicating a deeper water, low diversity variant of the Fauna.

3.1.7 Laurentia

The low diversity (five taxa) *Hirnantia* Fauna was reported from the Percé region, Québec (Lespérance and Sheehan, 1976). It is dominated by *Plectothyrella* (44.5% of the entire number of brachiopods), followed by *Eostropheodonta* (21.3%), *Hirnantia* (19.4%), *Kinnella* (11.4%), and *Dalmanella* (3.3%).

3.1.8 Lhasa Terrane

There are no additional data on the medium-diversity *Hirnantia* Fauna from central Xizang (Lhasa Terrane) since the study of Rong and Xu (1987) published in a Chinese journal. Based on three samples collected, the fauna is dominated by *Hirnantia* (26.4% of the whole fauna), *Paromalomena* (22.1%), *Cliftonia* (18.2%), and *Kinnella* (17.3%), with *Leptaena* (=their *Leptaenopoma*), *Eostropheodonta*

(=their *Aphanomena*), *Aegiromena*, *Dalmanella*, *Dysprosorthis* (=their *Horderleyella*) and *Plectothyrella* amongst others. *Horderleyella xainzaensis* Rong and Xu, 1987, is regarded as a junior synonym of *Dysprosorthis sinensis* Rong, 1984, a species from the Kuanyinchiao Bed (middle Hirnantian) of Yichang, Hubei, indicating a close faunal relationship between Lhasa and South China during the end Ordovician.

3.1.9 Marginal Laurentia

3.1.9.1 Maine, Northeastern United States By courtesy of the late Dr R.B. Neuman, the four Hirnantian brachiopod collections from Maine housed in the US Geological Survey were examined by J.Y. Rong in 1987 and 1997 (see Appendix I-A for identifications). This unit in northern Maine (Neuman, 1968) is characterized by a typical *Hirnantia* Fauna including *Hirnantia*, *Dalmanella*, *Kinnella*, *Cliftonia*, *Plectothyrella*, *Hindella*, and *Eostropheodonta*. Strikingly, they are associated with some rare, relatively deeper-water taxa, e.g. *Leangella*, *Skenidioides* and *Epitomyonia*, which are scarcely known in the *Hirnantia* Fauna elsewhere.

3.1.9.2 Girvan, Southern Scotland, UK Harper (2006) monographed a brachiopod fauna of the High Mains Sandstone yielding *Hirnantia sagittifera*, associated with some relic elements, such as *Plaesiomys*, *Platystrophia* and *Hypsiptycha* from shallow water facies on the margin of Laurentia (Harper, 1981). The dominance of *Hindella* (68% of the whole assemblage in number) and occurrence of *Hirnantia* (9.1%) at the locality H_2 are most striking, and the associated cosmopolitan *Fardenia*, *Hindella* and *Eostropheodonta* (41% at the locality H_1) are common characteristics of the *Hirnantia* Fauna.

3.1.10 New Zealand

A brachiopod faunule from the Wangapeka Valley, northernmost part of South Island was considered a *Hirnantia* Fauna based on the presence of *Leptaena* (most abundant), *Eostropheodonta*, *Cliftonia*, *Plectothyrella*?, and a few others, associated with *Mucronaspis mucronata* (Cocks and Cooper, 2004) The fossils are difficult to collect and the specimens are relatively few in number and poorly preserved since the rocks have undergone several phases of tectonic deformation, and many are unidentifiable shell fragments. The collection, however, is significant for Hirnantian biogeography, as the location is so remote from other coeval faunas.

3.1.11 Perunica

The high-diversity *Hirnantia* Fauna in Bohemia is the eponymous flagship of the Kosov Province. Apart from those taxa characteristic of the fauna (Marek and Havlíček, 1967), there are some local elements, e.g., *Giraldibella*, *Ravozetina* and *Comatopoma* of the orthides. Mergl (1986) and Havlíček (1994) described some new taxa of inarticulate brachiopods, e.g., *Rafangoflossa*, *Schizotretina*, *Tethyrete*, *Philhedra* and *Pseudopholidops* (=*Sanxiaella*) from the Kosov Formation (Hirnantian). The first three genera have not been found elsewhere. *Philhedra* sp. can be assigned to *Xenocrania*, which occurred widely also in the Hirnantian (Chen and Rong, 2019).

3.1.12 Precordillera, Argentina

Since Benedetto (1986) first documented the *Hirnantia* Fauna from the Don Braulio Formation of San Juan, Argentine Precordillera, more information on this fauna has been published (Benedetto, 1990,

2003; Sánchez *et al.*, 1991; Astini and Benedetto, 1992; Leone and Benedetto, 2019). It is a moderately diverse, typical *Hirnantia* Fauna that includes *Hirnantia*, *Dalmanella*, *Paromalomena*, *Eostropheodonta*, *Cliftonia*, *Plectothyrella* and others. It should be noted that the Precordillera was geographically separated from South America (Benedetto *et al.*, 2013), although the former was not far from the latter during the Hirnantian.

3.1.13 Qilian Terrane

A low diversity *Hirnantia* Fauna was documented from grey black sandy shale and argillaceous limestone in the Shichengzi Formation (Hirnantian) at Gulang, northern Qilian Mountains, Gansu, Northwest China (Qu, 1986). The fauna is composed of *Paromalomena*, *Aegiromena*, *Leptaena*, *Cliftonia*, and *Dysprosorthis*, accompanied by a higher diversity trilobite assemblage, e.g., *Mucronaspis* (*Songxites*) *wuningensis*, *Eoleonaspis*, *Decoroproetus*, *Diacanthaspis* and others. Components of the brachiopod fauna suggest a relatively deeper water regime (probably BA 4). Northern Qilian Mountains may belong to an independent terrane closer possibly to North China in the Ordovician and Silurian. To date, there is no record of the *Hirnantia* Fauna from North China.

3.1.14 Sibumasu Terrane

Since the pioneer work of Reed (1915), the *Hirnantia* Fauna is now known in some detail from the Northern Shan States and the Mandalay Division, Myanmar, Thailand, and western Yunnan, Southwest China.

3.1.14.1 Myanmar Cocks and Fortey (2002) restudied Reed's material and revised his taxonomic list

for the *Hirnantia* Fauna in the Northern Shan State, to include nine genera, such as *Dalmanella*, *Kinnella*, *Paromalomena*, and *Aegiromena*, associated with the trilobites *Mucronaspis* and *Eoleonaspis.* Based on new material collected, the *Kinnella–Paromalomena* Association has been proposed for the middle Hirnantian material in the Mandalay Division (Rong *et al.*, 2020). There occur the additional genera, '*Palaeoleptostrophia*', *Skenidioides*, *Mirorthis, Draborthis*, *Levenea*, *Toxorthis*, *Trucizetina*, *Plectothyrella*, *Hindella*, and most significantly *Hirnantia* itself. It provides more evidence for the presence of a high diversity, typical *Hirnantia* Fauna in the relatively deeper-water environments (lower BA 3) of northern Myanmar.

3.1.14.2 Western Yunnan A new collection of the upper part of the Wanyaoshu Formation (Hirnantian) at Luxi and Mangshi was obtained recently (Huang *et al.*, 2020a). They found a faunal sequence of shallow water to deeper water *Hirnantia* associations. The shallow one belongs to the typical *Hirnantia* Fauna with a medium diversity, whereas the deeper one is a representative of the *Hirnantia* Fauna, consisting of *Hirnantia* and *Kinnella*, along with *Anisopleurella*, *Aegiromena*, *Skenidioides*, *Templeella*, *Mirorthis* and others. *Skenidioides* is known to occur in the Mandalay Division, Myanmar. *Templeella* is known in the *Hirnantia* Fauna of England (Temple, 1968) and Chu–Ili (Nikitin *et al.*, 1980, see 2.1.6), upper Hirnantian of Zhejiang, East China (Rong *et al.*, 2013), and Aeronian of England (Temple, 1970) and West Mongolia (Rozman and Rong, 1993).

3.1.14.3 Thailand A relatively-low diversity, deep-water *Hirnantia* Fauna from the Wang Tong Formation contains six taxa, *Aegiromena* (77.3% of the sample), *Onniella*? (9.8%), *Hirnantia* (3%), *Cliftonia* (=their *Eospirigerina* sp.) (2.3%), *Mirorthis* (1.5%), and *Paromalomena* (0.8%), associated

with *Mucronaspis mucronata* (Cocks and Fortey, 1997). Noticeably, it is characterized by a nearly absolute dominance of *Aegiromena*, and by the absence of many typical taxa of the fauna, e.g., *Eostropheodonta*, *Hindella*, and *Plectothyrella*, indicating a relatively deeper water setting (BA4).

3.1.15 South America (the continent)

A low-diversity brachiopod association was reported from the Eusebio Ayala Formation in the Asunción area, the Paraná Basin by Benedetto *et al.* (2013). The fossils include four genera (*Arenorthis*, *Plectothyrella*?, *Eostropheodonta* and *Hindella*), which confirms the presence of a Bani–type assemblage in Paraguay, and may indicate faunal connections with the African basins. Moreover, they are associated with graptolites indicative of the *M. persculptus* Biozone. The brachiopod specimens identified as *Schizophoria*? from poorly stratified diamictites in the Cancaniri Formation in the central Subandean Ranges of Bolivia were revised as *Hirnantia sagittifera* by Benedetto *et al.* (1992). But this material has never been described nor illustrated.

3.1.16 South China

There is a condensed stratigraphical succession across the Ordovician and Silurian boundary in many areas of South China, as typified by the section at Wangjiawan, Yichang, Hubei, the GSSP of the Hirnantian Stage (Chen *et al.*, 2000, 2006). This succession consists of the Wufeng and Lungmachi formations (graptolite facies) and Kuanyinchiao Bed (shelly facies) in between yielding the *Hirnantia* Fauna. Analysis of the biostratigraphy and biodiversification of the *Hirnantia* Fauna (Rong *et al.*, 2002, 2018) and its α- and β- diversity changes (Li *et al.*, 2009; Zhan *et al.*, 2010, 2011) were provided in various studies. In addition, there occurs a limestone facies belt along the northern marginal region of the Qianzhong Oldland where brachiopods (Rong and Li, 1999) and corals (He, 1978, 1985; He *et al.*,

2007; Wang *et al.*, 2015, 2016a, b) are well represented. Their relationship with the *Hirnantia* Fauna will be discussed below in section 4.2. Most recently, a deep-water association of the fauna was documented from the uppermost Ordovician in northwestern Hunan and its palaeoecological implications were discussed by Rong *et al*. (2018). The deep-water, low diversity shelly assemblage is characterized by abundant *Aegiromena* and other rare elements (e.g., *Paromalomena*), along with the trilobites (*Mucronaspis*, *Eoleonaspis* and *Platycoryphe*). Synecological analysis shows that this assemblage lived on the upper Jiangnan Slope, adjacent to the southeast margin of the Upper Yangtze Region, and it belongs to the *Hirnantia* Fauna in cool and deep-water regimes (BA 4–5).

3.2. Data excluded from the dataset for the Hirnantia *Fauna*

The new and existing records of the *Hirnantia* Fauna are verified above. There are some other publications recording other brachiopod associations from the Hirnantian, e.g., those from Australia, Avalonia, Baltica, Kazakh Terranes, Laurentia, South Africa, South America, and Turkey. However, our revision indicates that some of those are not part of the *Hirnantia* Fauna, and thus are excluded from our dataset.

3.2.1 Wales, Avalonia

The brachiopods from the Wenallt Formation in the Garth area were first recorded by Williams and Wright (1981), but no updated information has been published. They assigned these high diversity brachiopods to the *Hirnantia* Fauna, because of the presence of *Cliftonia*, *Leptaena*, *Dalmanella*, *Hirnantia* (*H. sagittifera*), *Eostropheodonta* (*E. hirnantensis*), and *Hindella* (*H. crassa*), and two more,

Kinnella and *Plectothyrella* in the lower Ooids Member and upper Speckley Member respectively. These genera are indeed the most common constituents of the *Hirnantia* Fauna. However, there are many other genera, e.g., *Katastrophomena*, *Rhactomena*, *Kullervo*, *Glyptorthis*, *Platystrophia*, *Orthambonites*, *Sampo* and *Cyclospira*, in addition to many questionable or undetermined taxa, many of which are not known from the *Hirnantia* Fauna elsewhere. Some may be of pre–Hirnantian (Harper and Rong, 1995) or of late Hirnantian age (this paper). The brachiopods, invariably disarticulated with the majority of the valves broken, possibly accumulated in mixed/transported sediments under different conditions and were derived from discrete associations occupying a mosaic of niches. Williams and Wright (1981) pointed out that the overall average breakage of the identified brachiopods from the Ooid Member is 80%, if *Paracraniops* is ignored. Since the whole fauna was evidently mixed, and may have been derived from various sources, it is difficult to separate the typical *Hirnantia* Fauna from others. Moreover, the precise age of the two members remains unknown. Thus, the Garth brachiopods are provisionally excluded from our dataset for the *Hirnantia* Fauna.

The brachiopods from the Glyn Formation, Glyn Ceiriog District, North Wales include *Eodinobolus*, *Hirnantia*?, *Nicolella*, *Plaesiomys*, *Sampo*, *Schizophorella*, *Vellamo* and others, and were considered a representative of the *Hirnantia* Fauna or a latest Katian assemblage by Hiller (1980). Due to the presence of many of the Katian taxa, we support the latter correlation.

3.2.2 Chile

A single taxon, *Hindella crassa* is known to occur in Unit 2 of the Quebrada Ancha Formation of the southern Salar de Atacama, northern Chile (Niemeyer *et al.*, 2010). The species ranges from uppermost Katian, through Hirnantian to Rhuddanian. Thus, the age of the formation yielding *H.*

crassa in Chile cannot be constrained because of the absence of more reliable evidence.

3.2.3 Chingiz–Tarbagatai

The brachiopod assemblage of this region contains *Eostropheodonta*, *Leptaena*, *Cliftonia*, and *Dalmanella* (all cosmopolitan), associated with some immigrants (*Katastrophomena*, *Kozlowskites*, *Chonetoidea*, and *Epitomyonia*) (Popov and Cocks, 2017), which are essentially unknown elsewhere in the *Hirnantia* Fauna. It seems likely, thus, that the assemblage may not conform to the *Hirnantia* Fauna.

3.2.4 Gornyi Altay

Kulkov and Severgina (1987) recorded Hirnantian brachiopods containing species of *Kinnella*, *Eostropheodonta*, *Streptis*, *Brevilamnulella*, *Eospirigerina* and others from grey argillaceous limestones in the top part (20 m) of the Dorozhnin Horizon in Gornyi Altay. One of the authors (Jiayu Rong) examined this collection by courtesy of N. P. Kulkov in the Institute of Geology and Geophysics in Novosibirsk in the summer of 1990. A reassessment of these fossils indicates that the identifications of *Kinnella* and *Eostropheodonta* are questionable, the other genera are not observed in the typical *Hirnantia* Fauna, and the presence of pentamerids and atrypids seems to be the products of the upper Hirnantian. In addition, in the underlying strata, i.e., the top of the Orlodskaya Formation, all limestone, yield a possible *Thebesia*, a typical taxon of the Edgewood Fauna, but its serial sections are yet to be examined and its generic assignment cannot be confirmed.

3.2.5 Northwest Argentina

Benedetto *et al.* (2015) described a low diversity brachiopod association containing *Orbiculoidea*, *Dalmanella*, and *Paromalomena* from the top of the glacial-related Zapla Formation, northwest Argentina. The identification of *Paromalomena* remains doubtful due to the absence of the interiors. This association was assigned to a Hirnantian age partly based on the presence of chitinozoans of the *Spinachitina oulebsiri* Biozone (Benedetto *et al.*, 2015) and reassessed as a possible example of the lower *M. persculptus* Biozone (Wang *et al.*, 2019) but without reliable evidence.

3.2.6 Tasmania, Australia

A low-diversity association was listed as *Isorthis*, *Onnella*, *Hirnantia*? and *Eospirifer*? from the upper Westfield Sandstone on Tasmania. The unit was recorded as the earliest Silurian faunule (Laurie, 1991), but was later regarded as probably Hirnantian in age by Rong *et al.* (1994), concurred by Cocks and Cooper (2004). The brachiopods are not a *Hirnantia* Fauna and may have represented an entirely different assemblage.

3.2.7 Turkey

Sayar and Cocks (2012) described a so-called *Hirnantia* Fauna from southern Turkey, but whether or not it is represented by the key elements of the *Hirnantia* Fauna is much in doubt based on their illustrations. Subsequently, in the Ovacik area, southern Turkey, ice-related sediments of the Halevikdere Formation (Hirnantian) yielded a single brachiopod genus, *Mirorthis* that was considered to belong to the *Hirnantia* Fauna (Gutiérrez-Marco *et al.*, 2017). However, more evidence is needed to confirm the identity of this distinctive fauna in Turkey.

4. Biostratigraphy and vertical distribution

Defining the vertical distribution of the *Hirnantia* Fauna is key to understanding its origin, distribution and extinction. Here we review the global correlation of the *Hirnantia* Fauna across a range of different water depths, latitudes and facies. Graptolites have formed the basis for reliable correlation of the Hirnantian rocks worldwide and to determine the age of the *Hirnantia* Fauna. In many areas of the world, continuous successions across the Ordovician and Silurian transition containing the *Hirnantia* Fauna have been reported with graptolites above and/or below. Significantly, amongst them, South China displays many well exposed sections through the Hirnantian Stage and a related palaeogeographical reconstruction is presented in Figure 2 (Appendix II).

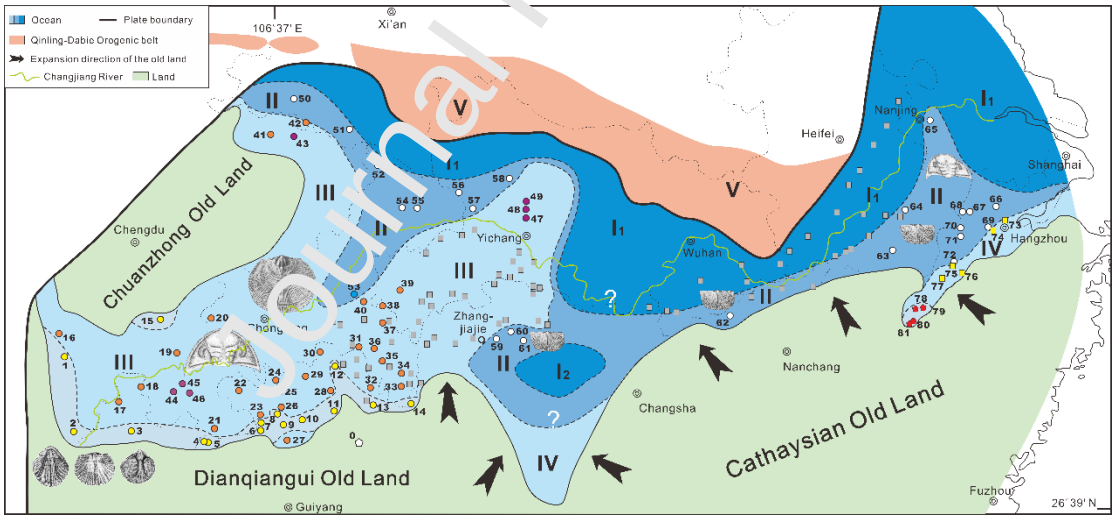

Fig. 2. Early–middle Hirnantian geographic reconstruction of South China with occurrences of the *Hirnantia* brachiopod Fauna, associated with the *Mucronaspis* trilobite Fauna. See Appendix II for detailed captions.

In the Upper Yangtze Region, the *Hirnantia* Fauna–bearing beds are usually sandwiched between

the Wufeng and Lungmachi formations, both graptolitic shales (Chen *et al.*, 2000, 2004), which enables the precise biostratigraphical correlation of the Ordovician–Silurian transition in South China (Fig. 3).

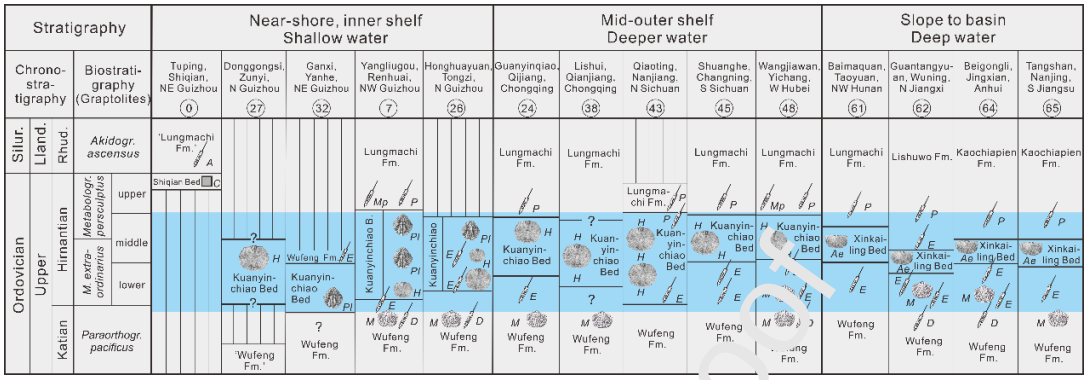

Fig. 3. Correlation chart of the Ordovician–Silurian boundary strata at selected sections in South China, including the successions of inner shelf, mid–outer shelf, and slope to basin, showing various stratigraphic positions of the *Hirnantia* Fauna–bearing beds. The Kuanyinchiao Bed, yielding near-shore, shallow water, low diversity communities of the *Hirnantia* Fauna, characterized by the *Dalmanella–Plectothyrella* Community and its relatives lacking *Hirnantia* and *Kinnella* in carbonate facies (BA 2) (*Pl*), and mid–outer shelf, relatively deeper water, moderate to high diversity *Hirnantia* Fauna in mudstone and siltstone (BA 3) (*H*). The Xinkailing Bed, containing deep water, low diversity *Hirnantia* Fauna (*Ae*), typified by the dominance of *Aegiromena* lacking *Hirnantia* and *Kinnella*. This figure shows the occurrences of the graptolites, *Diceratograptus mirus* (*D*), *Metabolograptus extraordinarius* (*E*), *M. persculptus* (*P*), *M. parvulus* (*Mp*), and *A. ascensus* (*A*) (Li *et al.*, 1984; Yu *et al.*, 1984; Chen *et al.*, 2000, 2005; Rong *et al.*, 2002), associated with occurrences of the brachiopods *Manosia* (*M*) (Rong and Huang, 2019) and *Cathaysiorthis* (*C*) (Rong *et al.*, 2013). Numbers are as in Fig. 2.

Both regional and worldwide correlations show that a large number of the *Hirnantia* Fauna–

bearing beds are mostly within the lower–middle Hirnantian based on the underlying and overlying graptolites. Convincing data from conodonts in the *Hirnantia*–bearing beds are rare (Zhang and Barnes, 2004, 2007) and will be discussed below. The Hirnantian chitinozoans have been reported from Baltica, Laurentia and Avalonia, but not in the GSSP of the Hirnantian Stage in Wangjiawan, Yichang (e.g., Vandenbroucke *et al.*, 2005, 2008). Further work on these microfossils may yet provide more information on the biostratigraphic correlation of the *Hirnantia* Fauna–bearing strata.

4.1 Global correlation of the Hirnantia Fauna–bearing strata

A correlation chart of the Ordovician–Silurian boundary strata in the selected regions of the world is illustrated in Figure 4.

4.1.1 Correlation with part of the M. extraordinarius Biozone

To date, the lowest known *Hirnantia* Fauna–bearing unit, the Kuanyinchiao Bed, in South China is exposed at Ganxi, Yanhe, northeastern Guizhou. It yields the brachiopods *Leptaena*, *Paromalomena*, *Eostropheodonta*, *Fardenia*, and *Dalmanella* along with the trilobites *Mucronaspis* and *Otarion*. It is underlain by the Wufeng Formation in the *Tangyagraptus typicus* Subbiozone (=upper part of *Paraorthograptus pacificus* Biozone) and is overlain by a bed of black shale with graptolites indicative of the upper *M. extraordinarius* Biozone (Rong *et al.*, 2002). A similar situation is documented in a shallow water succession at Sanlangpu, Xixiang, southern Shaanxi (Yu *et al.*, 1986), and in a deep water setting at Guantangyuan, Wuning, northwestern Jiangxi (Yu *et al.*, 1984). Recently, a low diversity *Hirnantia* Fauna recorded from the top Králův Dvůr Formation was correlated with the highest Katian, or more likely basal Hirnantian strata (Mergl, 2011; Kraft *et al.*, 2015) (Figs 4).

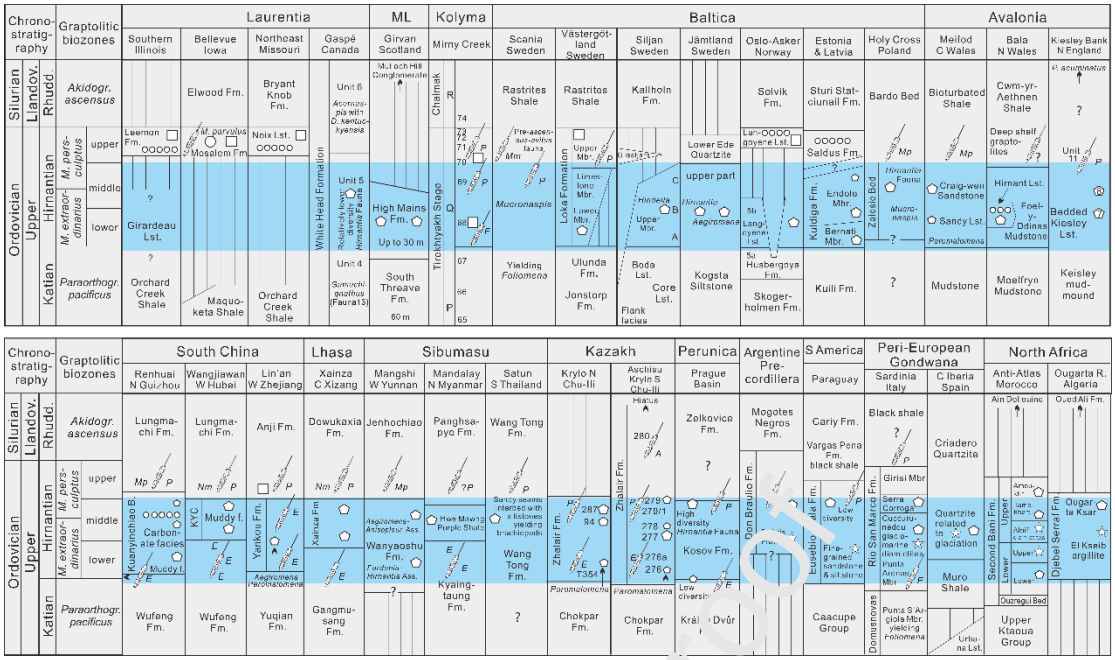

Fig. 4. Global correlation chart of biostratigraphy and lithostratigraphy across the Ordovician and Silurian boundary. Laurentia: Illinois, Iowa, and Missouri (Barnes and Bergström, 1988; Elias and Young, 1998; Loydell *et al.*, 2002; Stott and Jin, 2007; Bergström *et al.*, 2012b); Percé, Québec (Lespérance, 1988). Marginal Laurentia: Girvan, Scotland (Harper, 1981, 2006). Baltica: Jämtland (Dahlqvist *et al.*, 2010), Scania (Koren *et al.* 2003), Siljan (Suzuki *et al.*, 2009; Ebbestad *et al.*, 2015; Kröger *et al.*, 2015), and Västergötland (Bergström, 1968; Bergström and Bergström, 1996), Sweden; Oslo–Asker Region, Norway (Cocks, 1982; Brenchley and Cocks, 1982; Bockelie *et al.*, 2017); Estonia–Latvia (Harper and Hints, 2016; Hints and Harper, 2015); Holy Cross Mountains, Poland (Masiak *et al.*, 2003). Avalonia: Meifod, C Wales (Brenchley *et al.*, 2006; Schmitz and Bergström, 2007; Blackett *et al.*, 2009), Bala, N Wales (Temple, 1965; Brenchley and Cullen, 1984; Vandenbroucke *et al.*, 2008); Westmorland, N England (Temple, 1968; Wright, 1985, 1988; Cocks, 2008), UK. South China (Chen *et al.*, 2000; Rong *et al.*, 2002, 2013, 2018; Zhang *et al.*, 2007). Lhasa: Xainza, C Xizang (Rong and Xu, 1987). Sibumasu: Mangshi, western Yunnna (Fang *et al.*, 2018; Huang *et al.*, 2020a, c); Mandalay, Myanmar (Chen *et al.*, 2020; Rong *et al.*, 2020); Satun, S Thailand (Cocks and Fortey, 1997). Kazakh: Chu–Ili (Nikitin *et al.*, 1980). Perunica: Prague Basin, Bohemia (Štorch and Loydell, 1996; Štorch *et al.*, 1989, 2019). Argentine Precordillera (Sánchez *et al.*, 1991; Rickards *et al.*, 1996; Benedetto, 2003; Halpern *et al.*, 2014). South America: Bolivia and Paraguay (Benedetto *et al.*, 2013, 2014). European peri–Gondwana: Sardinia, Italy (Štorch and Leone, 2003); Central Iberia, Spain (Villas *et al.*, 1999; Sutcliffe *et al.*, 2001). North Africa: Anti–Atlas, Morocco

(Paris *et al.*, 1990; Sutcliffe *et al.*, 2001; Loi *et al.*, 2010; Colmenar *et al.*, 2015, 2018); Ougarta Range, Algeria (Popov *et al.*, 2019). *E. Metabolograptus extraordinarius*; *P. M. persculptus*; *Mp. M. parvulus*; *Nm. Normalograptus minor.* Note that the Borenshult fauna from Östergötland, Sweden, within fine grained, sparry skeletal grainstones is coeval with the oolitic limestone of the Skultorp Member in the middle Loka Formation (Bergström *et al.*, 2012a); Harper and Hints (2016) suggested that the Hirnantian Carbon Isotope Excursion (HICE) corresponds to the Skultorp Member and the upper Loka Formation, and the lower member is missing in the Borenshult core.

4.1.2 Faunas overlain by the M. persculptus Biozone

In many areas of the world, the *Hirnantia* Fauna is reported to be overlain by the *M. persculptus* Biozone. For example, in Västergötland, Sweden, the *Hirnantia* Fauna–bearing beds are well developed and overlain by strata yielding graptolites correlative of the *M. persculptus* Biozone (Bergström, 1968) There is a high diversity, distinctive fauna, from Keisley, Cumbria, England (Temple, 1968), which is overlain by the *M. persculptus* Biozone (Wright, 1985, 1988) (Fig. 4). Then these brachiopod fauna–bearing beds were correlated mostly with the *M. extraordinarius* Biozone.

Alternatively, the *Hirnantia* Fauna–bearing beds that are overlain by the *M. persculptus* Biozone may straddle the interface between the *M. extraordinarius* and *M. persculptus* biozones. For example, in various sections of Yichang, western Hubei, the basal part of the Lungmachi Formation yields *M. persculptus*, associated with *M. parvulus*, *Neodiplograptus shanchongensis*, and others, indicating the upper part of the *M. persculptus* biozone (Chen *et al*., 2005; Štorch *et al*., 2019). The *Hirnantia* Fauna–bearing beds in this area is underlain by graptolites, indicative of middle part of the *M. extraordinarius* Biozone. In northwestern Guizhou, the Kuanyinchiao Bed at Yangliugou, Renhuai contains the *Dalmanella-Plectothyrella* community, belonging to a low diversity *Hirnantia* Fauna (Rong and Li, 1999). The underlying Wufeng Formation yields *M. extraordinarius* and *N. ojsuensis* that represent the

level of the basal *M. extraordinarius* Biozone (see further discussion in 3.2). The graptolites *M. parvulus* and others occur from the overlying basal Lungmachi Formation, suggestive of the upper portion of the *M. persculptus* Biozone.

In the Holy Cross Mountains, southern Poland, a layer containing the graptolites *M. parvulus* and *M.* cf. *persculptus* overlies the Zalesie Beds (Masiak *et al.*, 2003) from which a moderate diversity, typical *Hirnantia* Fauna was identified (Temple, 1965). In Mangshi, southwestern Yunnan (Sibumasu Terrane), the Wanyaoshu Formation yielding the *Hirnantia* Fauna is overlain by the basal black shale in which *M. parvulus* occurs (Fang *et al*., 2017). These graptolitic layers may represent a level indicative of the upper portion of the *M. persculptus* Biozone (Štorch *et al*., 2019).

Another graptolite *Normalograptus minor* (Huang) is also stratigraphically important for age determination. It was first known from the basal 5 cm black shale of the Dewukaxia Formation (*M. persculptus* Biozone), immediately above the Xainza Bed yielding the *Hirnantia* Fauna in Xainza, Central Xizang (Lhasa Terrane). *N. minor* was also recorded from the same level in Hubei, Guizhou, and Zhejiang, South China (Chen *et al*., 2005; Muir *et al*., 2020), the Dob's Linn GSSP section in Scotland (Fan *et al*., 2005), and the pre-*ascensus-avitus* Fauna of Scania, southern Sweden (Koren *et al*., 2003). Thus, it appears to indicate a level of the upper part of the *M. persculptus* Biozone (Štorch *et al*., 2019) (Fig. 4).

4.1.3 Faunas associated with graptolites indicative of the lower M. persculptus *Biozone*

The *Hirnantia* Fauna has been recorded along with graptolites suggestive of the *M. persculptus* Biozone in some regions. In Bohemia, a high-diversity *Hirnantia* Fauna occurs in the uppermost Kosov Formation (Marek and Havlíček, 1967; Havlíček, 1989). *M. persculptus* (=formerly *Glyptograptus*

bohemicus Marek, in Štorch and Loydell, 1996) co-occurs with this fauna (Štorch, 1982, 1986, 1988, 2006; Štorch and Mergl, 1989; Štorch *et al.*, 2019). There is a sharp interface (firm ground as recorded in Štorch, 2006) between the Kosov Formation and the Silurian black shale that was interpreted as a paraconformity due to a gap in sedimentation spanning the upper *M. persculptus* Biozone to lower *A. ascensus* Biozone (Štorch *et al.*, 2019). If this is correct, the *Hirnantia* Fauna in Bohemia is more likely within the lower part of the *M. persculptus* Biozone, rather than the whole range of that biozone.

A newly established graptolite *M. parvulus* Biozone corresponds with the upper *M. persculptus* Biozone, including the pre-*A. ascensus* interval with an *N. avitus* Fauna (Koren *et al.*, 2003) below the First Appearance Datums (FADs) of *A. ascensus*, in some regions, for example Estana, northeastern Spain, Poland, Austria, Scania, Welsh Basin, Scotland and others (Melchin *et al.*, 2012; Štorch *et al.*, 2019). Below the *M. parvulus* Biozone, there occurs locally a representative of the *Hirnantia* Fauna and the trilobite *Mucronaspis*, in some areas of the Peri–Gondwanan Palaeoplate (Štorch *et al.*, 2019) (Fig. 4).

The Durben Horizon (lower Zhalair Formation) in Chu–Ili, Kazakh Terranes is correlated with both the *M. extraordinarius* and *M. perscuptus* biozones (Apollonov *et al.*, 1980, 1988). The genus *Paromalomena* is the only element of the *Hirnantia* Fauna present, and along with *Mucronaspis*, occurs in a deep water setting at Zhideli area in the lower Durben Horizon, indicating a correlation with *M. extraordinarius* Biozone. A moderate diversity *Hirnantia* Fauna occurs in the upper Durben Horizon, probably a correlative of the lower *M. persculptus* Biozone (Apollonov *et al.*, 1988).

The uppermost dark grey mudstone of the Don Braulio Formation (Hirnantian) in the Argentine Precordillera yields well-preserved brachiopods of the *Hirnantia* Fauna (Benedetto, 1986, 2003; Rickards *et al.*, 1996; Leone and Benedetto, 2019). The mudstone also contains a number of graptolite

specimens of the *M. persculptus* Biozone (Brussa *et al.*, 2003), indicating a correlation with the lower part of the latter biozone. Thus here, the *Hirnantia* Fauna can be correlated with the upper *M. extraordinarius* and the lower *M. persculptus* biozones (Leone and Benedetto, 2019).

There are many stratigraphic levels that appear to be marked by regressive, usually erosional, surfaces followed by terminal Ordovician black sediments deposited during subsequent global sea-level rise, in England (Brenchley *et al.*, 2006), Sweden (Kröger *et al.*, 2015), and Morocco possibly extending to upper Hirnantian? (Sutcliffe *et al.*, 2001; Colmenar *et al.*, 2018), or alternatively, the upper part of the Hirnantian Stage appears to be missing. Correlations of the Hirnantian rocks in Morocco and Algeria are tentatively illustrated in Figure 4 since they are partially based on the occurrence of a moderate diversity *Hirnantia* Fauna (Colmenar *et al.*, 2018). More work is needed before a more precise correlation of these regions can be established.

The above discussion demonstrates that the *Hirnantia* Fauna–bearing beds are diachronous across different sites, latitudes, facies, and depths in various degrees, rather than being synchronous as claimed by Wang *et al.* (2019). For the great majority, the fauna is constrained within the lower–middle Hirnantian, suggestive of a cool-water environment during the major Gondwanan glaciation, in contrast with the succeeding warm water environment accompanied by a marked glacio-eustatic sea-level rise in the late Hirnantian and afterwards.

4.2 Correlation between the carbonate facies in South China and Baltica

In South China, relatively thick Hirnantian carbonates, dominated by limestone, with the occasional presence of oolites and/or oncolites, occur in the Kuanyinchiao Bed, indicating near-shore,

shallow water settings in northern Guizhou and western Sichuan (Fig. 2). Some representative sections are selected herein for discussion.

As mentioned above, the middle–upper parts of Kuanyinchiao Bed (carbonates) at Yangliugou, Renhuai, northern Guizhou yield a rich, low diversity brachiopod fauna, formerly named the *Dalmanella testudinaria–Dorytreta longicrura* Community (Rong and Li, 1999). *D. testudinaria* is the most common brachiopod taxon; *D. longicrura* is herein revised as a junior synonym of *Plectothyrella crassicostis* (Dalman); therefore, the fauna is re-named the *Dalmanella–Plectothyrella* (simply *DP*) Community. These carbonate rocks can be correlated with the upper *M. extraordinarius* to lower *M. persculptus* biozones (Figs 3, 5).

The terminal Ordovician carbonates are well exposed in Bijie, northern Guizhou (Fig. 5), which was also close to the northern margin of the Qianzhong Oldland. Three sections across the Ordovician–Silurian boundary at Heitupo, Zhonggou west and east were examined by the present authors and are shown associated with ranges of the brachiopods, indicating a transitional change in both faunal composition and sedimentation (Fig. 5). The Heitupo section shows the thickest succession with a low diversity *Hirnantia* Fauna in the basal part of the Kuanyinchiao Bed and no benthos developed in the rest of the bed. There occurs a low diversity *Hirnantia* Fauna in mudstone of lower part of the Kuanyinchiao Bed at Zhonggou east and the *DP* Community in limestone of middle and upper parts of the Kuanyinchiao Bed at both sections in Zhonggou (see Fig. 5). Stratigraphically, it suggests a lithological change accompanied by a community transformation (from BA 3 to BA 2).

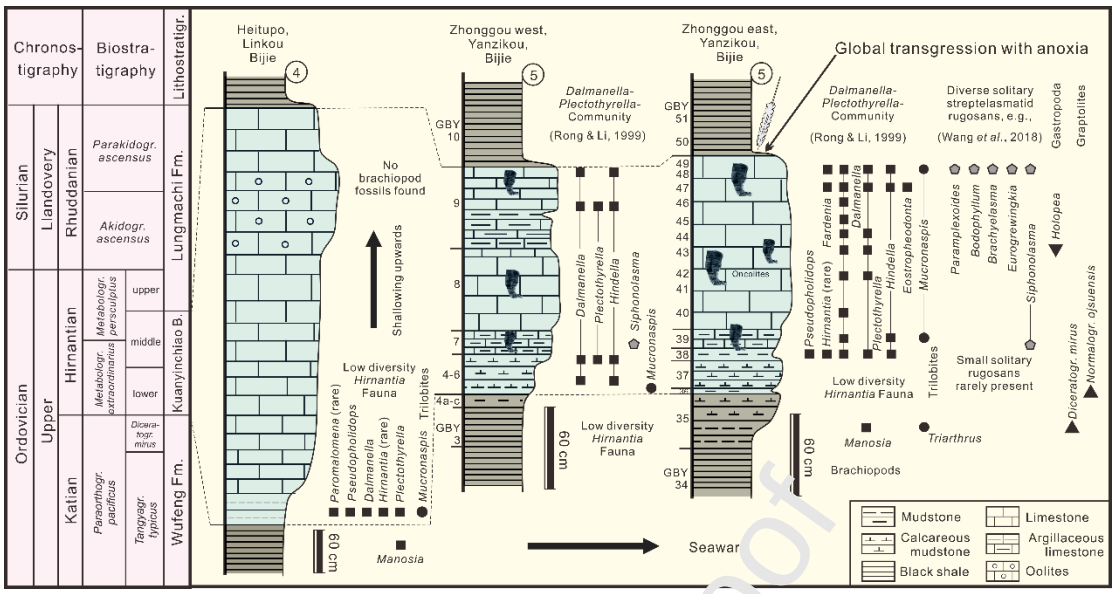

Fig. 5. Correlation of the uppermost Ordovician and lowest Silurian rocks of near-shore, carbonate facies at Heitupo, Zhonggou west and east, north of Bijie City town, northwestern Guizhou, South China with stratigraphic distribution of brachiopods, trilobites (Z.Y. Zhou), graptolites (X. Chen), and rugose corals (G.X. Wang). The numbers of the section refer to those in Fig. 2.

Not only vertically through the succession, but also laterally across different sections, the *Hirnantia* Fauna–bearing beds vary greatly in lithology and faunal composition within northern Guizhou (Fig. 6). Carbonate successions occur in Daijiagou, Tongzi (Zhan and Jin, 2007), where the ~2m-thick Kuanyinchiao Bed, consisting of argillaceous limestone intercalated with calcareous mudstone, yields a low diversity *Hirnantia* Fauna (mainly BA 2). The fauna, dominated by *Eostropheodonta*, associated with three common taxa of the *DP* Community, lacks *Hirnantia*, *Kinnella* and *Paromalomena*, and is named herein as the *Eostropheodonta–Dalmanella–Plectothyrella* (simply *EDP*) Association (Fig. 6). Based on the underlying graptolites, the Kuanyinchiao Bed in Tongzi is correlated with the middle–upper *M. extraordinarius* and the lower *M. persculptus* biozones (Figs 6, 7), which is overall coeval with those in Bijie and Renhuai counties.

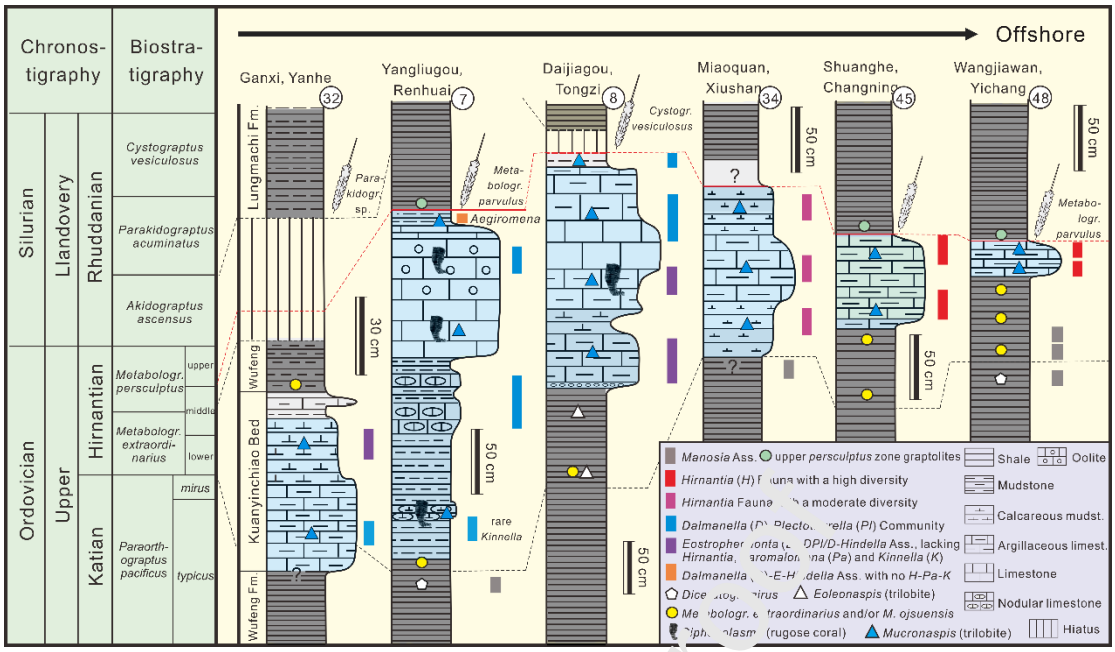

Fig. 6. Correlation of stratigraphic columns across the Ordovician and Silurian boundary along a near-shore to offshore transect in northern Guizhou, southern Chongqing, and western Hubei, Upper Yangtze Region, South China. The numbers refer to those in Fig. 2.

Northeastward of Daijiagou, the Kuanyinchiao Bed is well developed at Shanwangmiao, Honghuayuan, Tongzi, which provides one of the most classic sections through the end Ordovician interval (Chen *et al.*, 2000; Rong *et al.*, 2002) (Fig. 7). The shelly beds, totalling about 6 m thick, are composed mainly of mudstone, intercalated with several thickly bedded limestones, and are underlain by the middle part of the *M. extraordinarius* Biozone. The brachiopod fossils derived from 15 single-layers (from AFA 295–311c: Chen *et al.*, 2000) are re-investigated in this paper, and a newly updated stratigraphic distribution of the brachiopods is provided in Figure 7. In the basal part (AFA 295), there is a moderate diversity *Hirnantia* Fauna, dominated by *Cliftonia*, along with rare *Hirnantia*. In the succeeding layers (AFL 299, 300 and 302), *M. extraordinarius* and *N. ojsuensis* co-occur, indicating a level within the *M. extraordinarius* Biozone. Higher up (AFA 300–307), brachiopods

become significantly less diverse than those of AFA 295; *Hirnantia* and *Paromalomena* remain present, but decrease sharply in quantity and become obviously smaller in size (less than 5 mm wide) than those of AFA 295–299, indicating miniaturization under unsuitable environmental conditions. These two genera extended into AFA 307 and then disappeared. Changes of *Hirnantia* and *Paromalomena* in quantity and shell size indicate an improvement of environmental conditions, e.g., warmer water. Following the disappearance of *Hirnantia* and *Paromalomena*, there occur *Dalmanella*, *Plectothyrella* and *Hindella*, three key constituents of the *DP* Community, and extend up to AFA 309, 310, and 311c, where *Eostropheodonta* becomes predominant (*EDP* Association). All these observations suggest that the brachiopod succession at Honghuayuan may have resulted from changes in water temperature and lithofacies (substrates): *DP* was dominant in carbonate rocks in Bijie and Renhuai, where the *DP* Community favoured clear water, whereas *Eostropheodonta* being dominant in mudstone was associated with *Dalmanella*, *Plectothyrella* and *Hindella* (*EDP* Association).

Farther to the east, an argillaceous carbonate succession at Miaoquan, Xiushan, southeastern Chongqing crops out. The Kuanyinchiao Bed here is composed mainly of argillaceous limestone. Rich brachiopods from three layers belong to the typical *Hirnantia* Fauna with a relatively high diversity (nearly 20 genera) which can be assigned to middle BA 3 (Fig. 7).

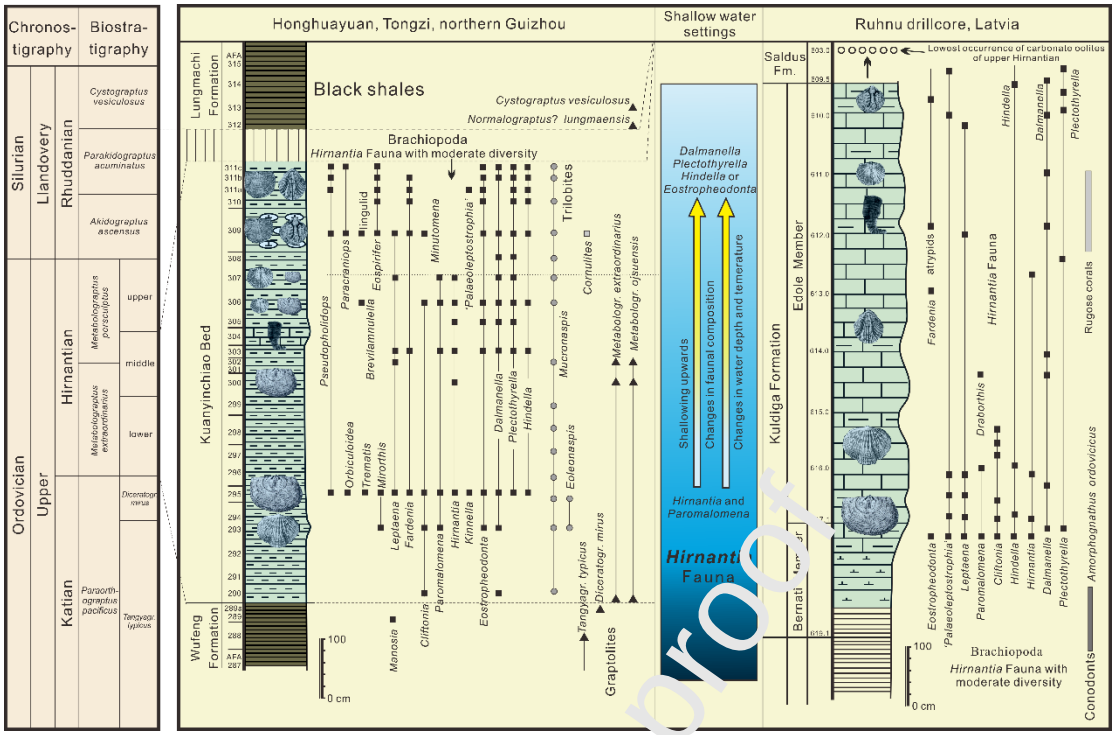

Fig. 7. Distribution of brachiopods, trilobites, graptolites and others through the Ordovician and Silurian boundary recorded in Honghuayuan, Tongzi, northern Guizhou, South China (updated and revised from Chen *et al.*, 2000) and in the Ruhnu core in East Baltica (Hints *et al.*, 2010; Harper and Hints, 2016). The brachiopod occurrences in the two sections are similar to each other in a complex scenario of changes in composition of the *Hirnantia* Fauna. The central diagram shows a relationship of two parts of the Fauna: 1) lower–middle part composed mainly of a relatively higher diversity of the Fauna is typified by the presence of *Hirnantia* and *Paromalomena*, associated with *Dalmanella* (*D*), *Plectothyrella* (*P*), *Hindella* (*H*) and others; 2) upper part composed of a relatively low diversity of the Fauna is dominated by the presence of *D*, *P*, *H* or *Eostropheodonta*, and lacking *Hirnantia* and *Paromalomena*.

The *DP* Community is herein assigned to the *Hirnantia* Fauna, rather than to the succeeding Edgewood-Cathay Fauna for the following reasons:

1. The *DP* Community comprises three of the most distinctive taxa *D. testudinaria*, *P. crassicostis*, and *H. crassa* that are common in the typical *Hirnantia* Fauna, indicating a reasonable assignment to the Fauna, but contrasting with the Edgewood Fauna in the carbonate facies of Laurentia and Baltica where only different species of *Dalmanella* and *Hindella* may be present.

2. The *DP* Community is stratigraphically lower than the Edgewood-Cathay Fauna–bearing beds and may be a product of the prolonged process of the later stage of the glaciation. It is also consistent with the absence of distinctive, warm water brachiopods, e.g., *Brevilamnulella* (pentameride), *Thebesia* (rhynchonellide), *Eospirigerina* (atrypide), and *Eospirifer* (spiriferide), and the lack of tabulates (Wang *et al.*, 2016b, 2018), stromatoporoid sponges, reefs (Copper, 2001), and the conodont *Ozarkodina hassi* (Bergström *et al*., 2012b).

3. Although there are limestones with oolites and oncolites in the upper Kuanyinchiao Bed in northwestern Guizhou, it is speculated that shallow marine environments may have been somewhat warmer than deeper water settings during the crisis. Moreover, the main constituents of the *DP* Community may then have adapted to a wider range of substrates, including both siliciclastic and carbonate seafloors, whereas those like *Hirnantia*, *Kinnella*, and *Paromalomena* appeared to be constrained by the pure limy environments where carbonates were deposited.

4. The associated rugose corals, being of high diversity (He *et al.*, 2007; Wang *et al.*, 2014, 2016a, b) are dominated by the streptelasmatids (e.g., *Streptelasma*, a solitary, morphologically simple but variable, opportunistic, ecologic generalist) (Elias and Young, 2001), and some genera of this clade may survive the two phases of the crisis (Elias and Young, 1998; Elias *et al*., 2013).

Thus, the role of litho-facies was key to the partitioning of the various facets of Hirnantian brachiopod associations through the stage and across latitudes and water depths. It may be of particular

significance that the main taxa of the *DP* Community have been also reported from the Kuldiga Formation in Estonia and Latvia (Harper and Hints, 2016). The Kuldiga Formation is further subdivided into the Bernati Member (lower) and the Edole Member (upper) (Fig. 7). The *Hirnantia* Fauna from the lower Edole Member, suggests an early Hirnantian age; however, it was correlated with TBF 2 (lower *M. persculptus* Biozone) by Wang *et al.* (2019). Brachiopods of the upper Edole Member are dominated by key taxa of the *DP* Community and are characterized also by the absence of *Hirnantia*, *Kinnella* and *Paromalomena*. It is consistent with the presence of the conodont *Amorphognathus ordovicicus* in the middle part of the Kuldiga Formation (Hints *et al.*, 2010) (Fig. 7).

5. Analysis of the *Hirnantia* Fauna

In this study, as noted above, network analysis (NA) rather than ordination and clustering techniques, is employed to investigate the geographical distribution of the Hirnantian brachiopod faunas (Huang *et al.*, 2016, 2018). This form of analysis is focused on the relationships between taxa, in this case their co-occurrence. Here NA is applied to the distribution of the *Hirnantia* Fauna and its variants.

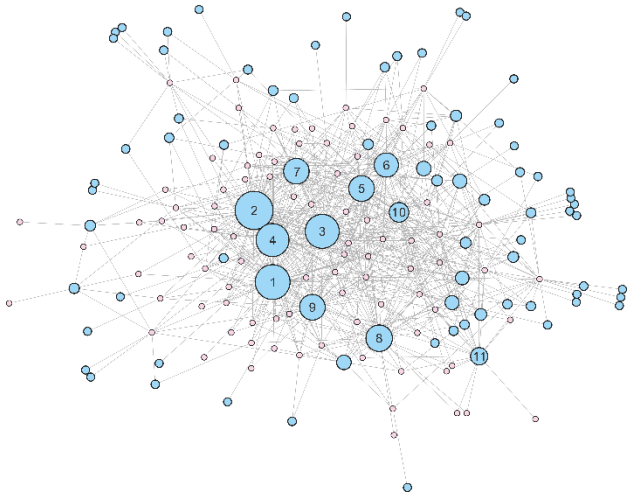

Fig. 8. Network diagram showing the connectivity for occurrences of genera of the global *Hirnantia* Fauna. Size of node indicates the number of occurrences at each node (Huang *et al*., 2016). The top 11 of the most common and distinctive genera are recognized. The nodes they represented are numbered and labeled. 1. *Hirnantia*, 2. *Eostropheodonta*, 3. *Dalmanella*, 4. *Plectothyrella*, 5. *Cliftonia*, 6. *Leptaena*, 7. *Hindella*, 8. *Paromalomena*, 9. *Kinnella*, 10. *Fardenia*, 11. *Aegiromena*.

For recognition of the core elements of the *Hirnantia* Fauna, generic analysis is required. The network diagram of the global *Hirnantia* Fauna is constructed based on data from 89 localities or samples with 82 genera captured from the global fauna (Fig. 8). The out degree of the network is calculated and visualized by the size of nodes of genera. The largest 11 nodes represent 11 genera (13% of the total) known from 8–14 regions, which are regarded as the most common, distinctive components of the fauna. There are ten genera (12%) known from 4–7 regions; and 59 genera (72%) recorded from 1–3 regions (Figs 9 and 10). The new dataset shows the considerable variability and complexity of the *Hirnantia* Fauna in many aspects, with a large variety of features in terms of abundance, composition, diversity, and community; some genera may be common in an association or, elsewhere, otherwise rare or absent in deference to others.

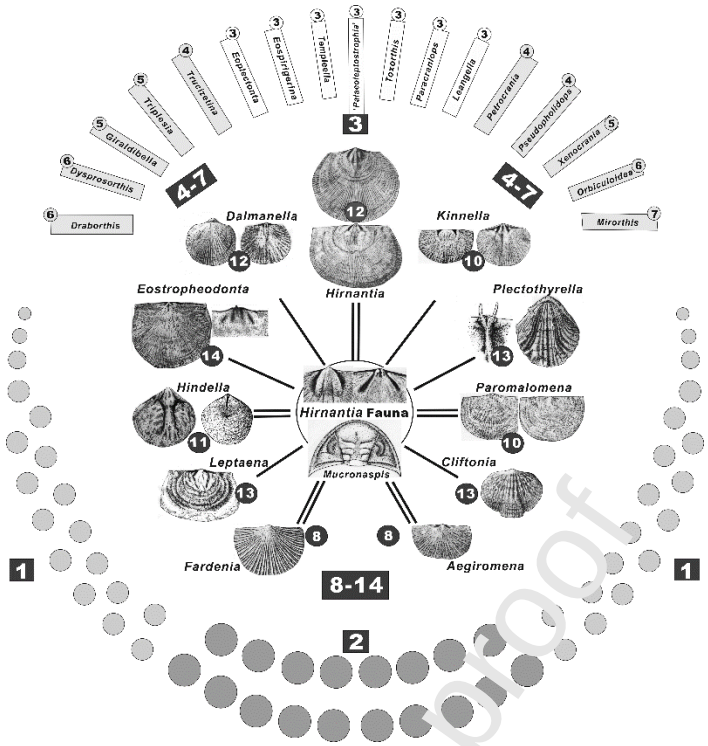

Fig. 9. Genera from the *Hirnantia* Fauna with occurrence numbers recorded in various palaeoplates or terranes. 8–14: the most common and distinctive genera known from 8–14 palaeogeographical units; 4–7 and 3: genera recorded in 4–7 and 3 units respectively; the others from 2 units or a single unit are omitted.

The number of genera included in the NA analysis is less than that in Sheehan and Coorough (1990), Rong *et al.* (2006), Harper *et al.* (2013), and Rasmussen (2014). This is because the present revision of the fauna has exposed some synonyms and excluded many taxa with a question mark and those indeterminate taxa from the dataset (Appendix I-A). The updated data are thus more reliable and the results should be more robust.

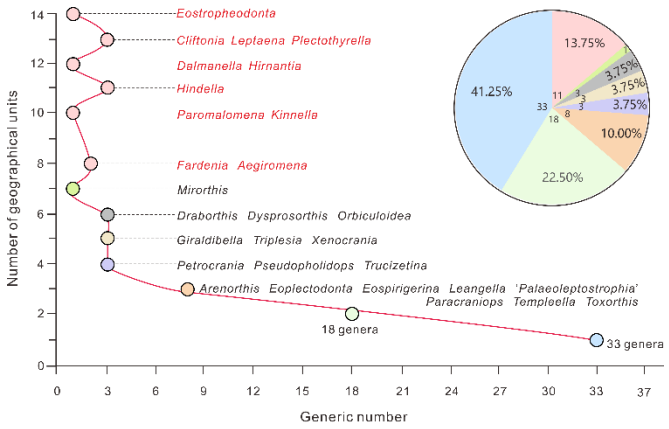

Fig. 10. Diagram showing numbers of geographical units where the brachiopod genera of the global *Hirnantia* Fauna are recorded in lower–middle Hirnantian strata.

5.1 Composition

Three subphyla of the Brachiopoda occur in the *Hirnantia* Fauna. The linguliforms and craniiforms comprise minor and rare, but distinctive components with generally a low diversity. The linguliforms, one of the major constituents of the Cambrian Evolutionary Fauna are very rare in the shallow water representatives of the fauna. The craniiforms, diversified in the Late Ordovician (Popov *et al.*, 2013), are represented by *Pseudopholidops* (craniopsides) and *Xenocrania* (craniides), as the two most common inarticulate brachiopods. The rhynchonelliforms are overwhelmingly dominant in the Fauna that is characterized by Orthida and Strophomenida, the absence of trimerellides, and a deficit in pentamerides and atrypides, with one or two common genera of orthotetides, rhynchonellides, and athyridides. Generic composition within the fauna can be categorized into the following four groups:

5.1.1 Most common, distinctive genera known from 8–14 geographical units

Sheehan and Coorough (1990) suggested that five to six occurrences for each genus may define

cosmopolitan taxa. In view of the database, we recommend that the occurrence in eight or more geographical units (palaeoplates or terranes) signal a genuine cosmopolitan form, and thus, eleven most common genera are recognized for the *Hirnantia* Fauna (Fig. 9). Each of the genera may be abundant, fairly common, rare, or even absent in a particular community, but co-occur with others at many sites, although there remain six to eight core taxa in the *Hirnantia* Fauna, as already noted by some authors (Amsden, 1974; Rong and Harper, 1988; Sheehan, 2001; Cocks and Cooper, 2004; Harper *et al.*, 2013; Harper and Hints, 2016).

Among these genera, four subgroups are recognized: 1. *Hirnantia*, *Kinnella* and *Paromalomena*, with their own species, are known as key taxa in the typical *Hirnantia* Fauna, and mostly from siliciclastic facies with calcareous sediments, indicating a strong preference for argillaceous limestone and mudstone/siltstone. 2. *Dalmanella*, *Plectothyrella* and *Hindella* occur both in mudstone/siltstone and limestone facies; they are less common in deeper water, siliciclastic sediments, but commonly dominate in shallower water carbonate facies. For shallow water settings, *Dalmanella* is the typical example and is the most common genus in the fauna in many places, e.g., Chu–Ili (Nikitin *et al*., 1980), Estonia–Latvia (Harper and Hints, 2016), Perunica (Marek and Havlíček, 1967), and South China (Rong and Li, 1999) (Appendix III). 3. *Eostropheodonta* occurs on many kinds of substrates, but few in pure carbonate facies; and *Leptaena*, *Cliftonia*, and *Fardenia* may dominate rarer communities, such as *Leptaena* in New Zealand (Cocks and Cooper, 2004), *Cliftonia* which can be commonly associated with *Hindella* in Baltica (Norway and Estonia–Latvia; Hints and Harper, 2015) and Avalonia (Kildare, Ireland; Wright, 1968), and *Fardenia* in Baltica (Västergötland, Sweden; Bergström, 1968), or show rare indications of dominance (Appendix III). 4. *Aegiromena* is an important indicator for low diversity, deep-water communities within the *Hirnantia* Fauna where many other forms are missing, e.g.,

Thailand (Cocks and Fortey, 1997), Jämtland, Sweden (Dahlqvist *et al.*, 2010), and South China (Rong *et al.*, 2018), but also occurs in high diversity, relatively deeper water *Hirnantia* faunas, e.g., in the top of the Kuanyinchiao Bed, Changning, Sichuan (Li *et al.*, 2009) and Yichang, Hubei (Zeng *et al*., 2016), and the top of the Kosov Formation, Prague, Czech Republic (Marek and Havlíček, 1967).

Their own predominant occurrences are documented mostly from South China, Baltica and Avalonia that were mostly in the low latitudes during the Hirnantian crisis (see Appendix III).

5.1.2 Common genera known from 4–7 units

There occur ten genera known from 4–7 geographical units bearing the *Hirnantia* Fauna (Figs 9, 10). We have not listed the detailed distribution of each of these taxa, but it is worth highlighting some key examples. *Draborthis* and *Mirorthis*, two characteristic taxa confined to the Fauna are recorded from Avalonia, Baltica, Perunica, Sibumasu, and South China; and recently from European peri–Gondwana (Álvaro *et al.*, 2016; Colmenar *et al.*, 2018). *Draborthis* is never predominant in a particular association; whereas *Mirorthis* has its exceptions: e.g., 92% of the sample AFN 3049 in the Kuanyinchiao Bed at Shuanghe, Changning, southern Sichuan (Li *et al.*, 2009); 34% of the association in the Hirnant Bed in Bala, northern Wales (Temple, 1965), and common in the Ribeira do Braçal Formation, Portugal (Colmenar *et al.*, 2018). *Dysprosorthis*, *Trucizetina*, and *Xenocrania* (Chen and Rong, 2019), are uncommon yet distinctive taxa of the Fauna, known also from Avalonia, Baltica, Perunica, Sibumasu and South China.

5.1.3 Genera known from 1–3 units

A large number of forms, which make up the majority of the fauna are only reported from one to

three regions (Figs 9, 10). This group is composed of two subgroups. 1) The majority are declining forms that were common in the pre–Hirnantian, Late Ordovician and Silurian, but few in the crisis interval with a dramatically decreased population size and a fragmented distribution (Rong *et al.*, 2006). Following the first phase of the extinction, the *Foliomena* Fauna became extinct; whereas some genera, e.g., *Skenidioides* (protorthides); *Dolerorthis*, *Glyptorthis*, and *Epitomyonia* (orthides); and *Eoplectodonta* and *Leangella* (plectambonitoids) characterising deeper water associations survived in 'refugia', joined the Hirnantian fauna to varying degrees, and extended into the Silurian. 2) Endemic forms, e.g., *Minutomena* in South China and Sibumasu (Zeng *et al.*, 2016; Rong *et al.*, 2020), *Titanomena* in Baltica (Bergström, 1968), and *Rafanoglossa* in Bohemia (Havlíček, 1994), are rare in number, and became extinct after the crisis.

Some genera, e.g., *Christiania* and *Chonetoidea* are known in Maine; *Eochonetes*, *Hypsiptycha* and *Plaesiomys* on the Laurentian margin in Scotland (Harper, 1981); and *Rugosowerbyella* in Chu–Ili (Nikitin *et al.*, 1980) during the early–middle Hirnantian. These forms, Dead Clades Walking (DCWs) (Jablonski, 1986), occurred widely in the pre–Hirnantian Late Ordovician, and survived the phases of the extinction, but became extinct shortly afterwards.

5.2 Diversity

There were large variations in diversity of the *Hirnantia* Fauna, reflected in a number of different associations or communities across the globe. The diversity changes were driven by many factors, e.g., water depth, substrate, latitudes and geographical positions. Some patterns and trends are becoming clearer, but many need to be further evaluated with more material.

To date, the diversity ranges from as few as a single taxon up to 26 genera in particular associations. A high diversity is documented in South China, Perunica, Sibumasu and Baltica, such as Yichang, Hubei (26 genera, Rong, 1984; Zeng *et al.*, 2016); Bohemia (25, Marek and Havlíček, 1967); Mandalay, Myanmar (23, Rong *et al.*, 2020) and western Yunnan (23, Huang *et al.*, 2020c); Changning and Gongxian (22, this paper), Nanjiang and Xiushan (21, this paper), South China; and Latvia (20, Harper and Hints, 2016), all within low latitudes, and developed in deeper water settings, usually in higher stratigraphic levels. The Keisley brachiopod fauna for northern England has a high diversity, associated with many deeper water species (Temple, 1968).

The lowest-known level containing representatives of the *Hirnantia* Fauna, with a low diversity, occurs in the uppermost Katian to the lowest Hirnantian in South China (Rong *et al.*, 2002). In addition, it should be noted that there is a low diversity *Hirnantia* Fauna in carbonate facies at a higher stratigraphic level, developed in near-shore, shallow water settings, e.g., the middle–upper part of the Kuanyinchiao Bed at some places of Bijie and Renhuai, northern Guizhou. All those mentioned above indicate a complex scenario of environments during the crisis (more discussion below).

5.3 Faunal change

5.3.1 Change with water depth

A diagram showing the depth distribution of many genera selected from the *Hirnantia* Fauna is presented in Figure 11. It is largely based on the data from Baltica, Sibumasu and South China, where a depth gradient occurs across the regions from shallow-water to deep-water facies. Along the gradient, the diversity of the fauna evidently changed, even in a single section, e.g., Mangshi, western Yunnan

(Huang *et al.*, 2020c). A very similar picture was suggested by Rasmussen *et al.* (2012) especially for Sandbian–Katian brachiopods. The differences are likely due to the development of the fauna through different time intervals. In the Upper Yangtze Region, associations of the *Hirnantia* Fauna, if close to shoreline, have a low diversity, commonly from four to seven brachiopod taxa as shown by the *Whitfieldella* Association (inner BA 2) occurring in siliciclastic facies in Zunyi, northern Guizhou. More examples came from Estonia–Latvia (Hints and Harper, 2015) and Algeria (Popov *et al.*, 2019). Regarding occurrences in coquinas, a single genus usually is present, e.g., coquinas of *Hindella* or *Cliftonia* in early–middle Hirnantian carbonate facies (BA 2) from Norway (Brenchley and Cocks, 1982), Ireland (Wright, 1968), Siljan, Sweden (Rasmussen *et al.*, 2010) and Estonia–Latvia (Harper and Hints, 2016). Deeper on mid-shelf, the diversity increased significantly, from eight to more than 14 taxa (inner BA 3). Farther off-shore, more than 20 taxa are present (outer BA 3 to possibly upper BA 4), e.g., in Sibumasu and South China. Down slope and into basin, diversity was reduced to several taxa (BA 4–5);he most dominant member is *Aegiromena*, sometimes along with *Paromalomena* and others (Cocks and Fortey, 1997; Dahlqvist *et al.*, 2010;).

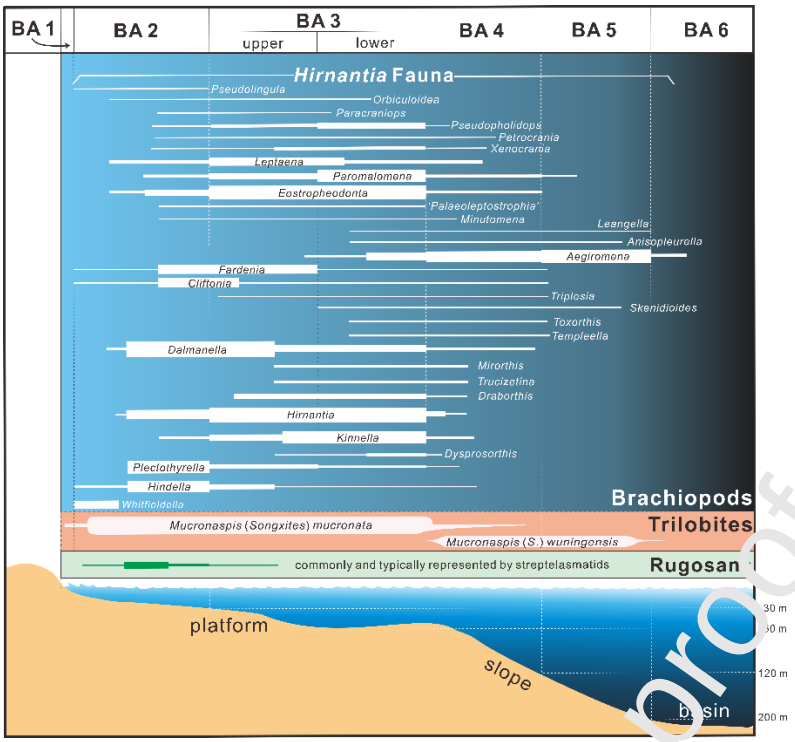

Fig. 11. Diagram showing water depth distribution of the selected common genera of the *Hirnantia* Fauna, associated with the trilobite *Mucronaspis* and common rugose corals recorded in current data based on the Benthic Assemblage Zones (BA) of Boucot (1975), data derived from Laurentia (Lespérance and Sheehan, 1976), Scotland (Harper, 1981), South China (Rong *et al.*, 2018; Zeng *et al.*, 2016), Sibumasu (Cocks and Fortey, 1997, 2002; Rong *et al.*, 2020; Huang *et al.*, 2020a, c), and Baltica (Cocks, 1982; Dahlqvist *et al.*, 2010; Harper and Hints, 2016).

5.3.2 Change with substrate

Fossils in the *Hirnantia* Fauna are commonly preserved as external and/or internal molds in fine-grained, calcareous siltstone, mudstone, and argillaceous limestone. The higher proportion of carbonates on the substrate, the fewer typical representatives of the *Hirnantia* Fauna occur. The fauna is only rarely preserved as silicified specimens recovered from biomicritic limestone in northwestern Guizhou (Rong and Li, 1999) and southwestern Sichuan, indicating that they may have been less

adapted to pure carbonate limy substrates than to other types. The coarse end of lithological spectrum is sandstone, where only a few of the fauna occur, e.g., Girvan, Scotland (Harper, 1981). A diagram is presented to show a range of various genera in different lithologies (Fig. 12).

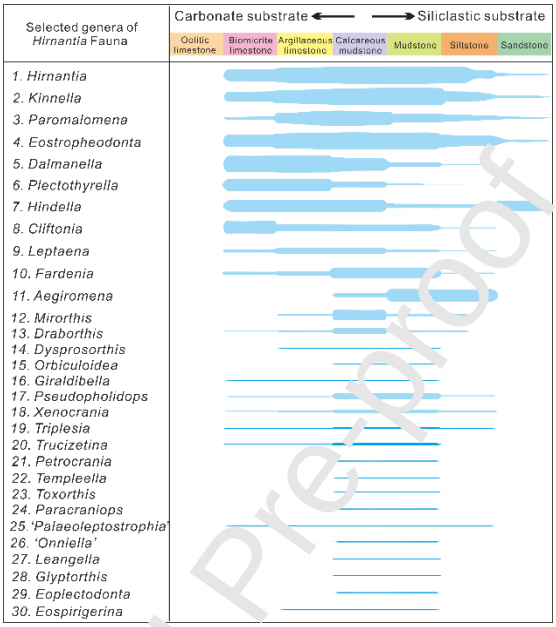

Fig. 12. Diagram showing lithological ranges of the selected 30 taxa of the *Hirnantia* Fauna that are related to various kinds of substrates. The thickness of the bars, here and elsewhere, indicates relative abundance of genera.

Regarding common genera, *Hirnantia*, *Kinnella*, *Paromalomena* and *Eostropheodonta* are known mostly from siliciclastic rocks, suggesting a preference for muddy and silty substrates (Fig. 12); *Dalmanella*, *Plectothyrella*, *Hindella*, and *Cliftonia* have a wider spectrum of occurrences than the four genera above and occur in both carbonate and siliciclastic facies. For example, *Dalmanella* is known from biomicrite limestone, argillaceous limestone, mudstone, and siltstone, and commonly dominates its host communities in Perunica (Marek and Havlíček, 1967), Kazakhstan (Nikitin *et al.*, 1980), South China (e.g., Rong and Li, 1999) and Estonia–Latvia (Harper and Hints, 2016). In sandstone, *Hirnantia*

and *Hindella* co-occur, whereas *Dalmanella* and *Plectothyrella* disappear (Harper, 1981). The other common taxa, e.g., *Leptaena* and *Fardenia*, are mostly recorded in siliciclastic facies, but vary greatly in their abundance (Fig. 12).

5.3.3 Change across latitude

Based on the latest reconstruction of Hirnantian global paleogeography (Torsvik and Cocks, 2017) (Fig. 1) the *Hirnantia* Fauna in fact occurred in the low latitudes (0°–30°): Sibumasu, South China, Alax, and Qilian of the northern hemisphere and Laurentia, Baltica, Avalonia, Perunica, Lhasa and Chu–Ili of southern hemisphere, middle latitudes (30°–60°: New Zealand, Argentine Precordillera, and European peri–Gondwana), and high latitudes (60°–90°: North Africa) (Fig. 13). However, in the northern hemisphere, the fauna is known only from the eastern part, e.g., South China and Sibumasu, rather than in the western part, e.g., Kolyma (Koren and Sobolevskaya, 2008), Urals (Antoshkina and Shmeleva, 2018), Altai–Sayan (Sennikov *et al.*, 2014), and part of Laurentia with related terranes, particularly not exceeding north of 30°N. The Kolyma Terrane, for example, contains lower Hirnantian carbonate strata, yielding low diversity brachiopods (e.g., *Thebesia* and *Eoplectodonta*) (Koren and Sobolevskaya, 2008), presumably a precursor of the Edgewood Fauna. This may have been related to water temperature, and/or the lack of oceanic currents bearing the larvae of the taxa of the *Hirnantia* Fauna. Alternatively, it may have had an equivalent of the *Hirnantia* Fauna, as the trilobite *Mucronaspis mucronata* occurs in the middle Hirnantian rocks in Altai–Sayan region (Sennikov *et al.*, 2014).

Perunica was previously assigned to middle latitude in southern hemisphere (Fatka and Mergl, 2009; Melchin *et al.*, 2013; Torsvik and Cocks, 2017; Štorch *et al.*, 2019), and was also placed at low

latitudes during the Late Ordovician (Villas *et al*., 1999). It is now regarded as the southern margin of the low latitude, which is supported by the faunal evidence with the highest diversity of the fauna, showing close similarity with those on low latitude South China.

The eleven most common genera are from both high and low–mid latitudes, except some genera. In the Hirnantian, *Dalmanella* and *Leptaena* seem to be known basically from low latitudes, but a single specimen of *Leptaena*? sp. has recently been recorded for the first time from an association assignable to the *Hirnantia* Fauna in Algeria (Popov *et al.*, 2019).

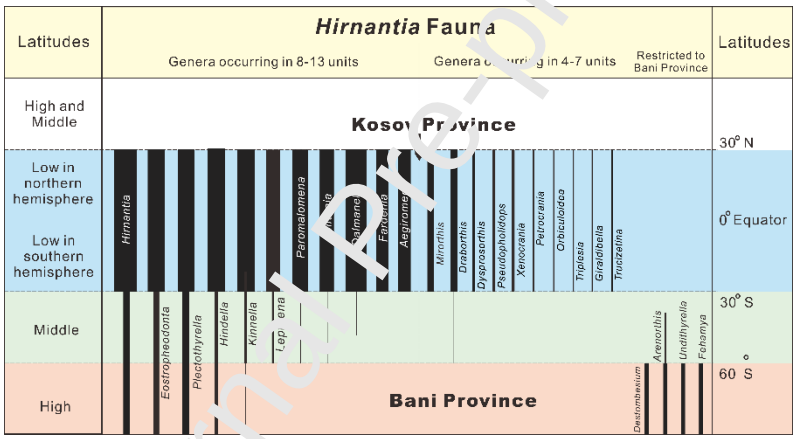

Fig. 13. Showing latitudinal distribution of common and distinctive genera of the *Hirnantia* Fauna in the early–middle Hirnantian based on the global reconstruction of Torsvik and Cocks (2017). Thickness of the bars represents relative abundance of genera.

5.3.4 Change with geographical position

The *Hirnantia* Fauna located in a marginal belt on a palaeoplate or terrane may have more faunal communication with other regions. For example, the Fauna in Girvan, Scotland (Harper, 1981), a marginal area of the Laurentia, bears some elements in common with taxa of the Laurentian type. Another example in Chu–Ili, a terrane in the tropical zone, where some elements like *Anisopleurella*,

Rugosowerbyella and *Templeella* are associated with the common constituents of *Hirnantia* Fauna, which may indicate a more flexible pattern of communication facilitated by oceanic currents (Huang *et al.*, 2020c).

Diversity changes in the *Hirnantia* Fauna can be related to many factors. We commonly assume that water depth, temperature and substrate may have played more important roles while geographical location should not be neglected (see 4.4).

5.4 Biogeography

To date, the *Hirnantia* Fauna has not been reported from the middle and high latitudes of the then northern hemisphere presumably due to the lack of available shallow marine settings (Fig. 1). The *Hirnantia* Fauna from low latitudes include those from Laurentia, Baltica, Avalonia, Chu–Ili of Kazakh, Lhasa and Perunica terranes in the southern hemisphere, and the Sibumasu, Qilian and Alax terranes, and the South China Palaeoplate in the northern hemisphere. All these regions were affected by cool/cold, well oxygenated oceanic currents carrying the larvae of members of the fauna along the western side of Gondwana and many blocks north of this large continent. The cosmopolitan and opportunistic nature of different elements of the *Hirnantia* Fauna may imply that there was a good oceanic circulation from the then pole to the tropics, and from southern to northern hemispheres, which was quite different from the more stagnant and stratified oceans during pre–Hirnantian, Late Ordovician and post-glaciation warming intervals.

5.4.1 Relationship of the Kosov and Bani provinces

The distinctions between the Kosov and Bani provinces were recognized by Rong and Harper (1988) based on: 1. A set of endemic forms in a low diversity *Hirnantia* Fauna from North Africa; 2. Fauna with *Hirnantia*, *Plectothyrella* and *Hindella* recorded in North Africa usually lacks any other typical forms of the Kosov Province. Recently more work on the fauna in North Africa and the European peri–Gondwana regions (in middle latitude, southern hemisphere) reveals that some genera (e.g., *Paromalomena*, *Kinnella*, *Draborthis* and *Mirorthis*) not only occur in France, Spain and Portugal, but also in North Africa (Villas *et al.*, 2006; Bernárdez *et al.*, 2014; Colmenar and Álvaro, 2015; Álvaro *et al.*, 2016; Colmenar *et al.*, 2018). This emphasises the similarity between these two provinces. However, the Bani Province is retained, because the occurrences of *Arenorthis*, *Destombesium*, *Fehamya*, and *Undithyrella*, as endemic forms in the Bani Province, indicating a marked provincialism (Fig. 13). Meanwhile, the European faunas of peri–Gondwana may link the Kosov and Bani provinces, as the transformation from cool to cold climates may have been gradual due to widespread climate change.

5.4.2 Placement of South Africa

Cocks *et al.* (1970) first recorded brachiopods (e.g., *Arenorthis*, *Eostropheodonta* and *Trematis*) from the Soom Shale Member of the Cedarberg Formation near Cape Town, South Africa, and compared them with the *Hirnantia* Fauna. These brachiopods were subsequently assigned to the Bani Province (Rong and Harper, 1988). Later, exceptionally-preserved fossils were recovered from the formation containing the inarticulates *Palaeoglossa* and *Kosoides* (Bassett *et al.*, 2009) which are unknown in the *Hirnantia* Fauna. The Cedarberg Formation was reported to be late Hirnantian in age (Vandenbroucke *et al.*, 2009; Gabbott *et al.*, 2017) and thus South Africa is excluded from the Bani

Province based on the faunal composition and the age determination of the Soom Shale and its brachiopods. Significantly, the brachiopods from this region, occurring in high latitudes within cooler water settings, also differ in composition from the Edgewood-Cathay Fauna that occupied low latitude, warmer water environments; the Soom Shale fauna may represent the separate biogeographic unit, a precursor of the Malvinokaffric Realm that evolved in the Silurian (Boucot, 1975). More information is required to develop this theme.

5.5 Epilogue

In conclusion, the *Hirnantia* Fauna is an adaptive combination of a variety of genera, including the eleven most common, distinctive taxa, associated with a wide range of other genera with different origins, and degrees of dominance. This resourceful and variable fauna appeared diachronously within the lower and middle Hirnantian and was distributed worldwide on a large number of palaeoplates or terranes, in cool/cold, different specific environments on various substrates and depths, across a range of latitudes during the early–middle Hirnantian.

6. Edgewood-Cathay Fauna and its equivalents

The term Edgewood Fauna was initially coined for a diverse shallow water shelly fauna including brachiopods from carbonate facies, typified by the Edgewood region, USA (Amsden, 1974). The brachiopods include *Biparetis*, '*Strophomena*', *Brevilamnulella*, *Eospirigerina*, *Stegerhynchus*, *Thebesia*, *Leptoskelidion*, and others, which are unknown from the *Hirnantia* Fauna. More records of

this fauna are known from the Manitoulin Formation of southern Ontario, Canada and the Mosalem Formation, Iowa, USA containing *Dolerorthis*, *Platystrophia*, *Dalmanella*, *Mendacella*, *Leptaena*, *Eoplectodonta*, *Fardenia* (including *Coolinia*), *Stegerhynchus*, *Thebesia*, *Orthorhynchillion*, *Zygospiraella*, *Sypharatrypa*, *Eospirigerina*, *Whitfieldella*, and others (Stott and Jin, 2007).

In addition, the fauna occurs in Baltica, Kolyma, Central Asia and others; e.g., the *Brevilamnulella* Association and *Thebesia* Association including *Leptoskelidion* in Oslo–Asker, Norway (Brenchley and Cocks, 1982), and the Borenshult fauna at Råssnäsudden, Östergötland, Sweden (Bergström and Bergström, 1996; Rong *et al.*, 2008b; Jin and Bergström, 2010). The Klinkenberg Formation, together with the basal Saelabonn Formation, Oslo Region, Norway were assigned to the Hirnantian (Heath and Owen, 1991; Nielsen and Harper, 2003; Stott and Jin, 2007), and contain low diversity brachiopod assemblages including *Dalmanella*, *Fardenia*, *Leptaena*, *Zygospiraella* and *Askerina* (Baarli, 2019). The corresponding rocks are developed in East Baltica, but the brachiopods are not well known (Harper and Hints, 2016). This fauna was also recorded from the Omulev Mountains, Kolyma with *Biparetis*, *Thebesia*, and *Eospirigerina* (Koren *et al.*, 1983; Koren and Sobolevskaya, 2008); in Gornyi Altai with *Thebesia*, *Brevilamnulella*, *Eospirigerina* and others (Kulkov and Severgina, 1987); and in Zeravshano–Gissar Mountains, Central Asia, with *Brevilamnulella*, *Thebesia*, *Eospirigerina*, *Whitfieldella* and others (Menakova, 1991) (see Appendix I-B).

Recently, a diverse brachiopod fauna was initially named the *Cathaysiorthis* Fauna, succeeding the *Hirnantia* Fauna, from siliciclastic facies in South China (Rong *et al.*, 2013, Huang *et al.*, 2019). This fauna, crossing the Ordovician–Silurian boundary, shares a number of taxa (see below) with the coeval Edgewood Fauna. To facilitate the discussion and comparison of these brachiopods from different facies, we propose the term Edgewood-Cathay Fauna to include the conventional Edgewood

Fauna and the Cathay Fauna (Fig. 14).

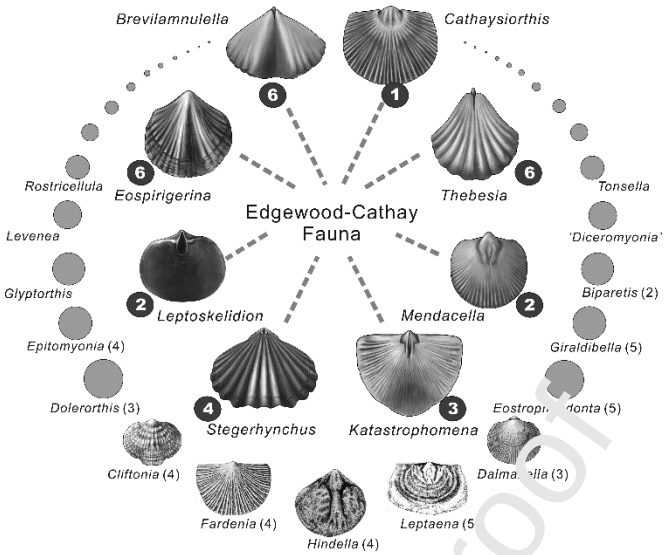

Fig. 14. Showing common and/or distinctive genera of the Edgewood-Cathay Fauna recorded in various palaeoplates and terranes in the late Hirnantian. Generic names recorded from a few units or a single unit are omitted.

Assemblages from these two facies are analyzed to show their relationships. To exclude the potential bias caused by bathymetric factors, only the collections from shallow water environments (BA 2–3) are, for the time being, selected for analysis. A total of some 70 genera occur within both faunas (see Appendix I-B). There are nearly half of the genera extended upwards from the underlying *Hirnantia* Fauna; others e.g., *Brevilamnulella*, *Eospirigerina*, *Mendacella*, and *Thebesia* include new arrivals.

Geographically, the Edgewood-Cathay Fauna is known to occur chiefly in low latitudes (e.g., Laurentia, Baltica, Kolyma, Siberia, Central Asia, South China and a few other places) (Fig. 15), and is associated with warm-water carbonates and siliciclasts, and does not co-occur with the *Hirnantia* Fauna.

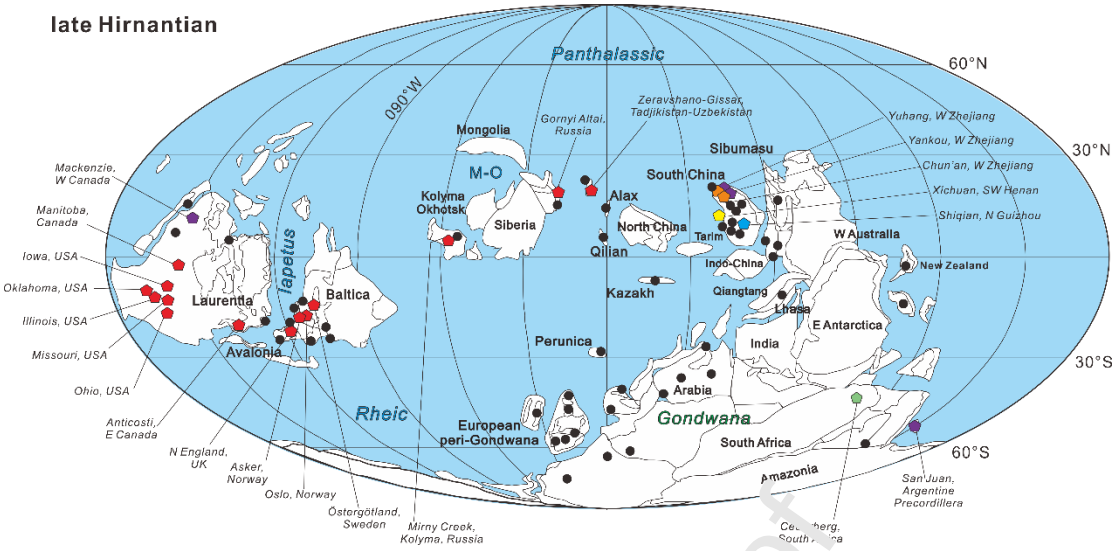

Fig. 15. Occurrences of the Edgewood-Cathay Fauna in late Hirnantian based on the global reconstruction of Torsvik and Cocks (2017). Red pentagon: the Edgewood Fauna known mainly in carbonate facies; brown pentagon: the Cathay Fauna in siliciclastic facies; yellow pentagon: a Rhuddanian *Cathaysiorthis* Fauna in eastern Qinling, SW Henan, Central China (Huang *et al*., 2019); black pentagon: deep water brachiopod assemblages; blue pentagon: presumably representing a high latitude brachiopod province in late Hirnantian to Rhuddanian; black cicles: black graptolitic shales in late Hirnantian and early Rhuddanian.

The resulting network diagram suggests a close relationship among the assemblages from both facies, although differences can be identified (Fig. 16). Globally, to date, the investigation of the Edgewood-Cathay Fauna has not been as comprehensive as that of the *Hirnantia* Fauna. Nevertheless, study of the Edgewood-Cathay Fauna may still reveal a basic scenario for the composition, diversity, palaeoecology, and palaeobiogeography of these late Hirnantian brachiopods based on the current dataset (Appendix I-B).

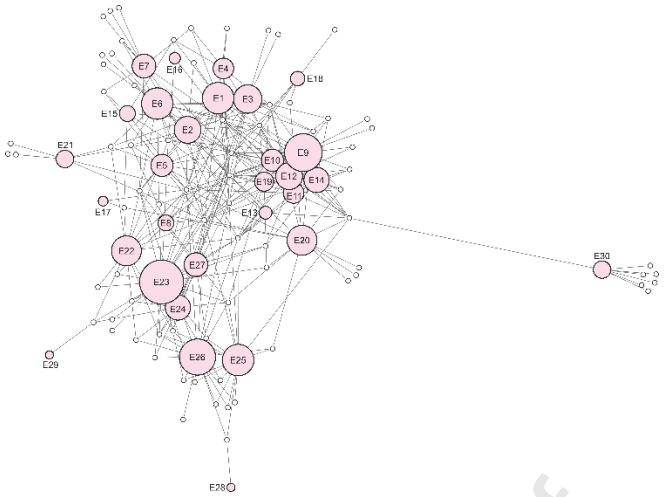

Fig. 16. Network analysis showing the connectivity for occurrences of genera and a close relationship between the Edgewood Fauna (E1–E21) and the Cathay Fauna (E22–E29). Size of node indicates the diversity of the collection that represented. Although many endemic taxa made the Cathay Fauna relatively independent, the clear boundary was not detected between the two faunas. The late Hirnantian deep water associations (E8, E28) are not included. E30 (South Africa) may presumably represent a high latitude brachiopod province in the late Hirnantian and early Rhuddanian.

The brachiopods form the basal part of the Skelgill Beds in the Lake District, England characterized by the atrypid "*Plectatrypa*" *flexuosa* (Marr and Nicholson, 1888; Brenchley and Cocks, 1982; Cocks, 2008), the basal part of the Becscie Formation on Anticosti Island (Bergström and Goldman, 2019), lower part of the Hilliste Member (the Juru Stage), Estonia (Stott and Jin, 2007; Rubel, 2011), and the Wulipo Bed, Meitan, northeastern Guizhou, South China (Wang *et al.*, 2020) were considered upper Hirnantian. But, more research on these brachiopod assemblages is required and are thus provisionally not included in the dataset for the Edgewood-Cathay Fauna.

6.1 Age determination

The Edgewood Fauna in the upper Hirnantian rocks in Sweden, Norway, Estonia, Kolyma, Canada and USA is associated with graptolites and conodonts (*Ozarkdina hassi*) indicative of (probably the upper part of) the *M. persculptus* Biozone (Bergström and Bergström, 1996; Loydell *et al.*, 2002; Stott and Jin, 2007; Koren and Sobolevskaya, 2008; Bergström *et al.*, 2012a, b, 2014; Demski *et al.*, 2015). The presence of *Metabolograptus parvulus* in the Wilhelmi Formation of Illinois and the Mosalem Formation of Iowa raises the possibility that the lowermost parts of the two formations are of late Ordovician age rather than of early Silurian age as previously thought (Loydell *et al.*, 2002).

The conodonts recovered indicate a late Hirnantian age for the Keel and Leemon formations (Bergström and Boucot, 1988) in which the typical Edgewood brachiopods occur; and the conodont *Ozarkodina hassi* was recorded from the uppermost Loka Formation in the East Baltica (Bergström *et al.*, 2012b; Männik and Viira, 2012) and from the upper Stonewall Formation of the Williston Basin and upper Port Nelson Formation of the Hudson Bay Basin, where a prominent positive $\delta^{13}C$ excursion (HICE) occurs and corresponds to the upper portion of the Hirnantian (Demski *et al.*, 2015).

The occurrences of the tabulates, e.g., heliolitids (*Propora*), favositids (*Palaeofavosites*), and halysitids (*Halysites*) in the conventional Edgewood Fauna are excellent indicators of a late Hirnantian age. With the exceptin of a few examples, the tabulates have not been encountered from the lower Hirnantian, but have been recorded from the upper Hirnantian rocks of Gornyi Altai (Yolkin *et al.*, 1988), Kolyma (Kaljo *et al.*, 2003; Koren and Sobolevskaya, 2008), Manitoba (Demski *et al.*, 2015), Mid–Continent (Elias *et al.*, 2013), Norway and Sweden (Brenchley and Cocks, 1982; Bergström and Bergström, 1996; Wang *et al.*, 2019), and South China (Wang *et al.*, 2014, 2015, 2016, 2017, 2019). In

the Oslo – Asker district, Norway, the tabulates are known to co-occur with the Edgewood brachiopods, *Brevilamnulella*, *Stegerhynchus*, and *Eospirigerina* from the top Hirnantian rocks (Brenchley and Cocks, 1982; Bockelie *et al.*, 2017). In South China, the Shiqian Bed (upper Hirnantian) in Shiqian, Guizhou yields tabulates (Wang *et al*., 2019; see 6.2.2).

The Hirnantian isotopic carbon excursion (HICE) was recognized (Kleffner *et al.* 2005; Bergström and Goldman, 2019 and therein). Bergström *et al.* (2012b) proposed that the HICE in the Laurentian Mid–Continent may correspond only to the falling segment, i.e. upper part of a complete HICE in the Cape Girardeau curve. Thus, the Leemon Formation yielding the Edgewood Fauna was assigned to the upper Hirnantian (Bergström *et al.*, 2006, 2012b). The Bowling Green Formation was dated as lowest Rhuddanian (Bergström *et al.*, 2012b), and yielded rich brachiopods that are similar to those of the aforementioned three formations. New $\delta^{13}C$ values confirm that the position of the *Brevilamnulella kjerulfi* coquinas in Siljan, Sweden (Kröger *et al.*, 2015) is located on the falling limb of the HICE, which also supports a late Hirnantian age (Bergström *et al.*, 2012; Männik and Viira, 2012).

The Cathay Fauna from the basal Anji Formation (AFL 68) at Wangjiaba, Yushan, northeastern Jiangxi was correlated with the *A. ascensus* Biozone, but is very similar to those of AFL 159-161 from Dakengwu, Chun'an, western Zhejiang, which was correlated with the same biozone (Rong *et al.*, 2013). Because associated chitinozoans (AFL 161) are characterized by the dominance of *Spinachitina verniersi*, along with *Belonechitina* cf. *postrobusta*, and Tang *et al.* (2012) noted the probability of a late Hirnantian age for the sample cannot be excluded, the AFL 159 and 161 fossils are included in the dataset for the late Hirnantian brachiopods (see 6.2.2 and Appendix I-B).

Thus, in view of the above data, the Edgewood-Cathay Fauna, as a whole, is stratigraphically higher than the *Hirnantia* Fauna (Rong and Harper, 1988; Rong *et al.*, 2013); it appeared immediately

after the second episode of the end-Ordovician extinction, and extended to the earliest Silurian (Huang *et al.*, 2019).

6.2 Distribution of the Edgewood-Cathay Fauna

6.2.1. Edgewood-Cathay Fauna in carbonate facies

There are strongly divergent opinions regarding the age of the Laframboise Member in the uppermost Ellis Bay Formation on Anticosti Island, and a definitive conclusion has not been reached on its precise stratigraphic position (e.g., Jin and Zhan, 2008; Kaljo *et al.*, 2008; Delabroye and Vecoli, 2010; Copper *et al.*, 2013). A so-called *Hirnantia* Fauna comprising *Hirnantia* sp. (Cocks and Copper, 1981) was recorded from Anticosti; but their *H.* sp. has been re-assigned to *Mendacella* by Jin and Zhan (2008). A few specimens identified as *H. sagittifera* occur in the Laframboise Member, and this species is associated with taxa not typical of the *Hirnantia* Fauna (Jin and Zhan, 2008). The brachiopods from this member include *Vinlandostrophia*, *Mendacella*, *Hirnantia*, *Furcitella*, *Fardenia* (including *Coolinia*), *Eostropheodonta* (=*Aphanomena*), *Eochonetes*, *Leptaena*, *Eostrophonella*, and *Hindella* (Dewing, 1999; Jin and Zhan, 2008; Copper *et al.*, 2013; Copper and Jin, 2014); five of them are cosmopolitan; many characteristic taxa of the *Hirnantia* Fauna and the trilobite *Mucronaspis* are absent. Geographically, Anticosti is close to Pérce, Québec where a *Hirnantia* Fauna was reported (Lespérance and Sheehan, 1976), yet strangely, a typical *Hirnantia* Fauna is lacking on Anticosti. Moreover, *Metabolograptus* cf. *parvulus* was identified from the basal Laframboise Member (Melchin, 2008) which was reported from the upper *M. persculptus* Biozone in Canadian Arctic (Melchin *et al.*, 1991). Its stratigraphic position is similar to that of *M. parvulus* from Iowa and Illinois in being just

below the base of the *O. hassi* Biozone (Bergström *et al.*, 2012b). Thus, Bergström *et al.* (2012b) proposed that there is a gap between this member and the underlying Lousy Cove Member, which, in their view, is correlated with the upper and basal Hirnantian respectively. Considering its composition and its age of probably late Hirnantian (e.g., Copper and Jin, 2014), brachiopod associations from the Laframboise Member are included in the dataset for the Edgewood-Cathay Fauna (Appendix I-B).

6.2.2. Edgewood-Cathay Fauna in siliciclastic facies

Recent work on the upper Hirnantian rocks in South China has revealed the occurrence of a rich, characteristic brachiopod fauna, initially named the *Cathaysiorthis* Fauna that inhabited shallow water environments (BA 2–3) (Rong *et al.*, 2013). At Wencheng, Chun'an, western Zhejiang, an association from the basal Anji Formation (AFL159 and 161: mudstone) includes many brachiopod taxa, such as *Katastrophomena*, *Levenea*, and *Mendacella* (the three being most abundant), associated with *Brevilamnulella*, *Cathaysiorthis*, *Eospirigerina*, *Fardenia*, *Glyptorthis*, *Leptaena*, *Thebesia* and *Whitfieldella* (see Appendix I-B). 'Edgewood' brachiopods from the basal Anji Formation (AEP 708-8: mudstone) at Yankou, Lin'an, Zhejiang (Zhang *et al.*, 2007) are represented by *Glyptorthis*, *Levenea*, *Brevilamnulella*, *Eospirigerina* and others, and are regarded as early representatives of the Edgewood-Cathay Fauna. Within the strata 27H (145 m thick) below the brachiopod–bearing layer, there are small, rare *Aegiromena* and a single specimen of *Paromalomena*, suggesting a deep-water, low diversity variant of the *Hirnantia* Fauna during early Hirnantian.

A near-shore, low diversity shelly faunule was reported from the Shiqian Bed of limestone intercalated with calcareous mudstone, north of Shiqian, northern Guizhou which is underlain by the Linhsiang Formation (middle Katian) and overlain by the 'Lungmachi Formation' (lowest Rhuddanian)

(Hu *et al.*, 1983; Wang *et al.*, 2015, 2016). The faunule in the calcareous mudstone yielded rare brachiopods characterized by *Cathaysiorthis* sp. (= '*Hirnantia*' sp. Pl. I, figs 3–7 of Hu *et al.*, 1983). The limestone yields the tabulates *Catenipora*, *Halysites* (=*Schedohalysites*), *Palaeofavosites*, *Propora*, and *Sibiriolites*, and the rugosans *Axiphoria*, *Brachyelasma*, *Eurogrewingkia*?, *Grewingkia*, and *Meitanolasma* (Wang *et al.*, 2014, 2015), indicating a remarkable similarity to the Edgewood coral fauna (Elias *et al*., 2013; Wang *et al*., 2017). Discovery of the conodont *Ozarkodina* aff. *hassi* from the Shiqian Bed (Wang and Aldridge, 2010) supports a late Hirnantian age (Wang *et al.*, 2016, 2018, 2019).

6.2.3 Edgewood-Cathay Fauna

Although the Edgewood Fauna and the Cathay Fauna possess some of its own characteristic genera resulted from different lithofacies and/or their different geographical ranges, there occur a number of genera mutual to, such as the pentamerides (*Brevilamnulella*), atrypides (*Eospirigerina*), rhynchonellides (*Thebesia*), strophomenids (*Katastrophomena*), dalmanelloids (*Mendacella*) and orthoids (*Dolerorthis*). They are basically unknown from the *Hirnantia* Fauna and are thought to be the products of post-glaciation conditions. Investigations demonstrate that the isolation of South China during Late Ordovician and Early Silurian was documented substantially (Wang *et al.*, 1984; Zhan and Cocks, 1998; Rong *et al.*, 2006; Rasmussen and Harper, 2011a) and may have led to a higher diversity and unusual provinciality in shallow water regimes, likely as an endemic center or a distinctive subprovince within the Edgewood-Cathay Fauna.

6.3 Deep water brachiopod associations

Several deep-water associations of late Hirnantian age were recorded in Laurentia, Baltica, South America, and South China; for example, the brachiopods *Epitomyonia*, *Brevilamnulella* and *Eospirigerina* in the Whitaker Formation (upper Hirnantian) in Mackenzie District, Canada (Jin and Chatterton, 1997), and the *Leangella–Dalmanitina* (*Songxites*) Assemblage from the Yankou Formation (upper *M. persculptus* Biozone) in Yuhang, Zhejiang (Rong *et al.*, 2008a), contain tiny, thin shelled taxa, and may have inhabited deep-water, in partially dysaerobic environments. A very sparse faunule with *Anisopleurella* and *Reuschella*? was reported from an unnamed unit within the *M. persculptus* Biozone in Sierra de Villicum, the Argentine Precordillera; the unit is likely of late Hirnantian age (Benedetto, 1987; Rickards *et al.*, 1996; Leone and Benedetto, 2019). In addition, the deep-water forms, e.g., *Chrustenopora*, *Mendacella*, *Jezercia*, *Epitomyonia*, *Dicoelosia*, and others, representing a significant assemblage, were discovered in Hirnantian–Rhuddanian boundary strata in Asker region, Norway (Baarli and Harper, 1986; Baarli, 2014).

The relationship between the above deep-water associations and the Edgewood-Cathay Fauna of shallow-water regime requires further investigation. More work might prove these associations as a lateral extension of the Fauna to the deep-water settings.

6.4 Comparison of the Edgewood-Cathay Fauna with the Hirnantia *Fauna*

Based on the revised, global data of Hirnantian brachiopods, a network diagram has been generated using Network Analysis (Figs 15–17). The network analysis of the combined dataset of the Edgewood-Cathay Fauna and the *Hirnantia* Fauna separates the collections into two distinctive groups (with only three exceptions, H55, E 28 and E30). The H55 site, representing a variant of the *Hirnantia*

Fauna from Girvan, Southern Scotland (Harper, 1981), contains some relic elements from shallow water facies on the margin of Laurentia, which may draw the node into the corner of the Edgewood-Cathay Fauna data group. On the other hand, the E30 site, the fauna from South Africa, at high palaeolatitudes, contains almost no data from the Fauna data group (Fig. 16). Here, the low diversity of the collection, absence of common elements of the Fauna, and a few typical taxa of the *Hirnantia* Fauna, group the collection with the upper Hirnantian, high latitude sites. In addition, E28 at Sanqiaobu, Deqing, Zhejiang Province contains only a deep-water genus *Aegiromena*.

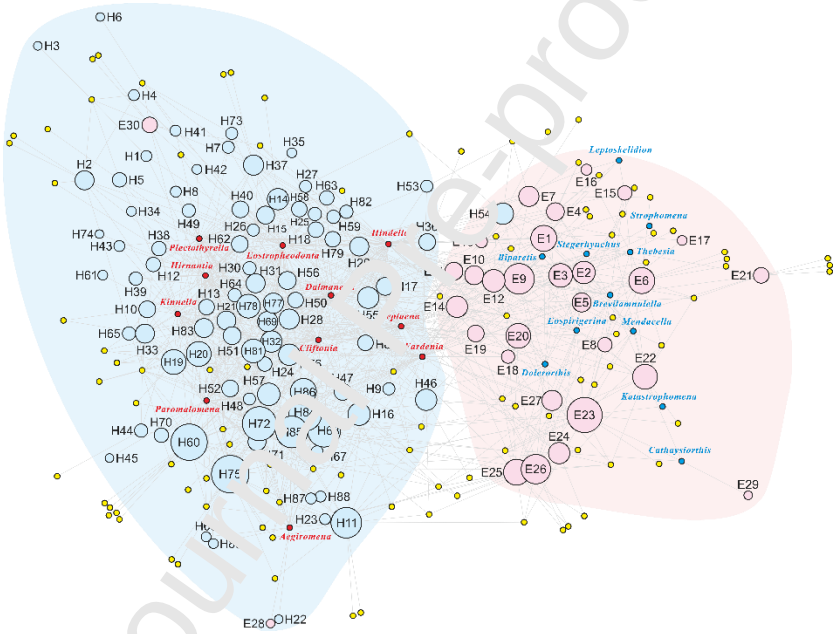

Fig. 17. Network analysis showing the differences between the *Hirnantia* Fauna (in blue and labeled beginning with 'H') and the Edgewood-Cathay Fauna (in light red and labeled beginning with 'E') (Huang *et al*., 2016). Size of node indicates the diversity of the collection that represented (see Appendix I). The collections can be separated into two distinctive groups with three exceptions, E28: Zhejiang, South China, E30: South Africa, and H54: Girvan, S Scotland.

The numbers of the order, superfamily, family and genera from the two faunas are presented in

Figure 18 for comparison. The both faunas are dominated by the orthides and strophomenides, totally occupying about 55% of the whole genera. Meanwhile, it is not surprising that there exist some mutual genera, e.g., *Dalmanella*, *Leptaena*, and *Hindella*, between the two faunas, but the species and predominance of each genus may be different.

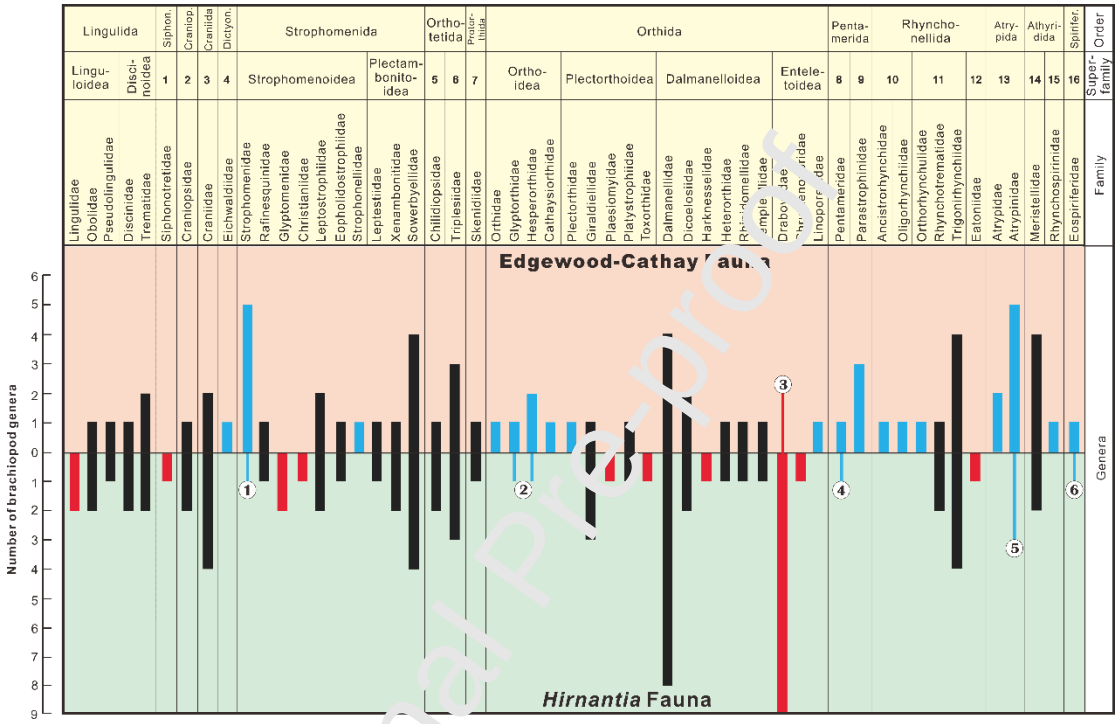

Fig. 18. Showing number of brachiopod genera in each family occurring in the *Hirnantia* Fauna and the Edgewood-Cathay Fauna. Numbered superfamilies include: 1 Siphonotretoidea, 2 Craniopsoidea, 3 Cranioidea, 4 Eichwaldioidea, 5 Chilidiopsoidea, 6 Triplesioidea, 7 Skenidioidea, 8 Pentameroidea, 9 Camerelloidea, 10 Ancistrorhynchoidea, 11 Rhynchotrematoidea, 12 Uncinuloidea, 13 Atrypoidea, 14 Meristelloidea, 15 Athyridoidea, 16 Cyrtioidea. Blue bar representing those only or mostly known in the Edgewood-Cathay Fauna; red bar representing those only or mostly known in the *Hirnantia* Fauna; black bar occurring in the both faunas. Circles: (1) No strophomenids in the *Hirnantia* Fauna with the exception of *Titanomena* (Bergström, 1968); orthoids (2), pentamerides (4) and spiriferides (6) very rarely and atrypides (5) rarely known in the *Hirnantia* Fauna; (3) draboviids rarely discovered in the

Edgewood-Cathay Fauna.

Figure 18 shows that many families and genera in the Edgewood-Cathay Fauna are not present in the *Hirnantia* Fauna, and vice versa. The essential differences between these two faunas are represented by the common occurrence of strophomenids and orthoids in the Edgewood-Cathay Faunas, which were basically absent in the *Hirnantia* Fauna. On the other hand, the enteletoids (particularly draboviids) are common in the *Hirnantia* Fauna, but much less in the Edgewood-Cathay Fauna in both quantity and diversity.

The pentamerides and atrypides are the most significant major groups within the Edgewood-Cathay Fauna, but are basically absent in the *Hirnantia* Fauna. *Brevilamnulella*, a virgianid, gave rise to the Silurian pentameroids (Jin and Copper, 2010; Harper *et al.*, 2013), and *Eospirigerina*, played a similar role for the early evolution of the Silurian atrypoid group. They are known from many palaeoplates or terranes in the late Hirnantian, indicating the presence of a warm water environment.

The Edgewood-Cathay Fauna in warm, shallow-water carbonate facies is significantly different from those in the same facies bearing a low diversity *Hirnantia* Fauna. The latter is usually dominated by *Dalmanella*, *Plectothyrella*, *Hindella* and/or *Cliftonia*, and inhabited relatively cool, shallow-water regimes.

7. Evolution of brachiopod faunas through the O–S transition

This section focuses on the evolution of the Hirnantian brachiopod faunas and attempts to locate the source of key taxa that gradually dominated the subsequent Silurian brachiopod faunas. The major

change in the brachiopods is now thought to occur at the boundary between middle and late Hirnantian. This was a major loss of taxonomic biodiversity, even though the ecological changes caused by the crisis only indicate the third- and fourth-level ecological magnitudes (Droser *et al.*, 2000; McGhee *et al.*, 2004, 2013).

7.1 Diversity and composition changes through the O–S transition

The events through the transition led to significant changes in diversity and composition of brachiopod faunas. The diversity curve shows a symmetrical pattern across the O–S boundary (Fig. 19). Brachiopod diversity is similar during: 1. Late Katian and Aeronian, 2. Early–middle Hirnantian and late Rhuddanian; and 3. Late Hirnantian and early Rhuddanian. This is interpreted as a delayed effect following the second Hirnantian wave of the crisis, supporting the conclusion that the changes provided a real test of the resilience and sustainability of the brachiopods (Harper *et al.*, 2017).

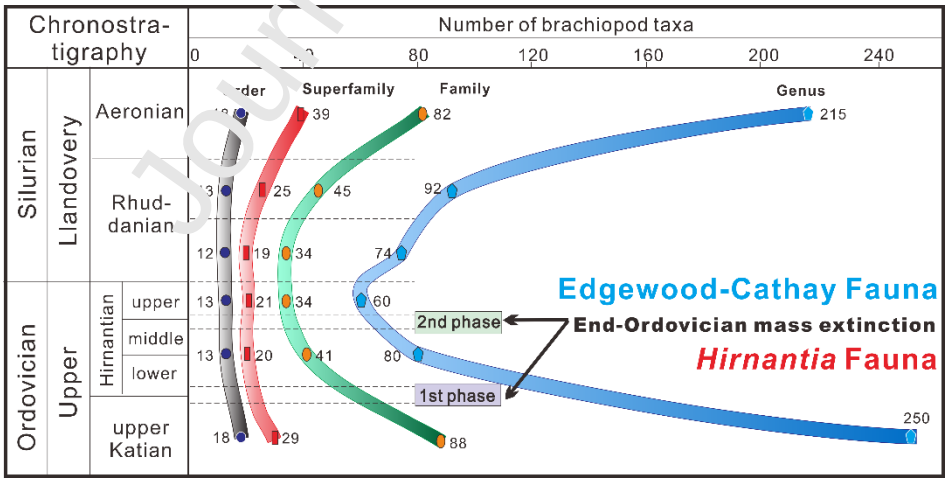

Fig. 19. Txonomic changes in brachiopod diversity through the Ordovician and Silurian transition. Basic data from Rong *et al.*, 2006; Harper *et al.*, 2013; Huang *et al.*, 2017 (upper Katian), this paper (Hirnantian), Cocks and Rong, 2008; Huang *et al.*, 2012, 2018; Copper and Jin, 2014 (Rhuddanian),

and Rong and Cocks, 2014 (Aeronian).

Our dataset reveals that the early–middle Hirnantian orthides are typified by the proliferation of two major clades: the dalmanellids and draboviids, while the others, e.g., the orthids and plectorthids that were common in pre–Hirnantian became rare. In the strophomenides, common in pre–Hirnantian Ordovician, only strophodontids and glyptomenids became common during the crisis; whereas many others were able to repopulate in the late Hirnantian. It demonstrates that the early evolutionary stage of the Silurian brachiopod faunas began in the late Hirnantian and early Rhuddanian (Fig. 20).

In the late Rhuddanian to Aeronian, more typical Silurian faunas occur, characterized by 1) pentamerides and atrypides that expanded substantially both in diversity and abundance, and became the most common, major groups; 2) athyridids and spiriferides were common in particular communities; 3) orthides and strophomenides gradually declined in dominance, except strophodontids; and 4) other groups variously continued to expand (Harper and Rong, 1995; Cocks and Rong, 2008; Rasmussen and Harper, 2011b; Huang *et al.*, 2012, 2017; Rong and Cocks, 2014; Rasmussen, 2014) (Fig. 20).

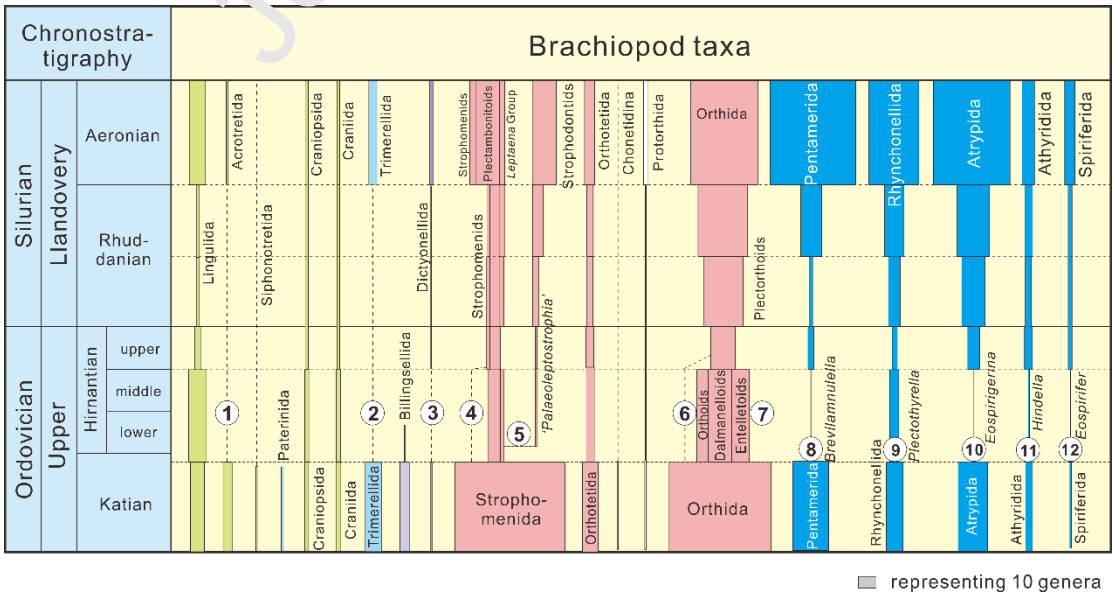

Fig. 20. Taxonomic changes in brachiopods at order and genus levels through upper Katian to Aeronian (basic data from: Popov and Holmer, 2000; Harper, 2000; Copper, 2002; Cocks and Rong, 2000, 2008; Boucot *et al.*, 2002; Savage, 2002; Alvarez and Rong, 2002; Rong *et al.*, 2006; Copper and Jin, 2014; Rong and Cocks, 2014; Huang *et al.*, 2018; the present study). During the early–middle Hirnantian: 1–4, Disappearances of the acrotretides, trimerellides, dictyonellides, and strophomenids; 5, An evolutionary transition from *Eostropheodonta* to '*Palaeoleptostrophia*' recorded in the same population; 6, Disappearance of plectorthoids; 7, Diversification of dalmanelloids and enteletoids; 8, Very rare occurrences of *Brevilamnulella* in the *Hirnantia* Fauna; 9, Rare representatives of rhynchonellides—*Plectothyrella*; 10, Rare occurrences of *Eospirigerina* (atrypides); 11, Rare representatives of athyridides—*Hindella*; 12, Very rare occurrences of *Eospirifer* in the *Hirnantia* Fauna which gave rise to the order Spiriferida.

7.2 Turnover of brachiopod faunas in terminal Ordovician

The evolution of brachiopods across the O–S transition is characterized by two major turnovers: 1. The replacement of warm-water brachiopod faunas by cold/cool-water faunas around the Katian–Hirnantian boundary, and 2. The latter in turn replaced by warm-water faunas in the late Hirnantian.

7.2.1 Demise of the Foliomena *Fauna and its equivalents*

During the latest Katian, the catastrophic impact severely affected in both shallow water, for example, the early virgianid pentamerides (large shelled, e.g., *Holorhynchus*: Rong and Harper, 1988; Hints, 1993; Beznosova, 2011, 2014 among others) and the rhynchonellides (e.g., *Altaethyrella*: Zhan

and Cocks, 1998; *Hiscobeccus*: Jin, 2001), and deep water *Foliomena* Fauna, usually associated with the *Cyclopyge* trilobite Fauna (Harper, 1981; Cocks and Rong, 1988; Rong *et al.*, 1999; Sheehan, 2001; Zhou *et al.*, 2004; Harper *et al.*, 2013; Zhan *et al.*, 2014; Finnegan *et al.*, 2017 and therein). Figure 21 shows the global occurrences of warm water biotas in low latitudes, including the large shelled virgianids which were replaced by a small shelled virgianid counterpart, the genus *Brevilamnulella* (Jin *et al*., 2007). The elimination of these shallow water faunas may have been caused by substantial sea-level lowering, habitat loss, and climate cooling; whereas the extinction of the *Foliomena*–*Cyclopyge* Fauna may represent loss of a distinctive deep-water biotope adapted to low-oxygen conditions widespread during the Boda Event (Boucot *et al*., 2013; Fortey and Cocks, 2005) and may have been resulted partially from an overturn of deep oceanic water.

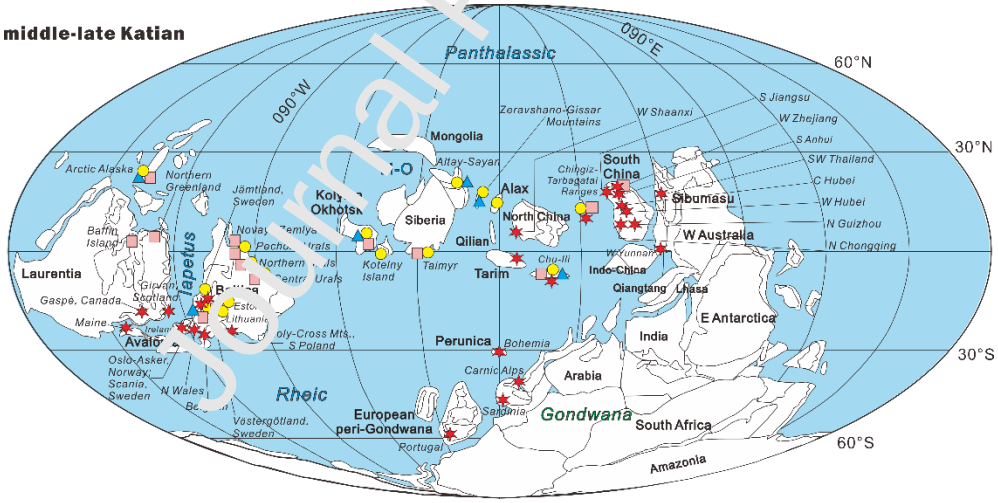

Fig. 21. Global occurrences of early virgianid brachiopods (chiefly from Rong and Boucot, 1998; Jin and Copper, 2000; Jin *et al*., 2006, 2007; Beznosova, 2014), associated with the *Foliomena* Fauna (red hexagon) (Rong *et al.*, 1999; Villas *et al*., 2002; Zhan and Jin, 2005; Zhan *et al.*, 2014; Colmenar *et al*., 2017) in middle–late Katian based on the global reconstruction of Torsvik and Cocks (2017). Blue triangle: *Brevilamnulella*; yellow circle: *Holorhynchus*; light purple square: *Proconchidium*, or

Tcherskidium, or *Deloprosopus*.

7.2.2 Establishment of the Hirnantia *Fauna*

The origin of the *Hirnantia* Fauna is still far from clear. To explore its origin, the source of the core genera and their distribution before the crisis should be scoped out in detail. The Fauna has thought to be descended from cool water Mediterranean associations (cf. Sheehan, 1979; Havlíček, 1989, 1990; Gutiérrez-Marco *et al.*, 2017), such as the draboviids (Colmenar *et al.*, 2013); *Hirnantia* and *Kinnella* were derived from Bohemia and *H. sagittifera* may have evolved from a species of *Drabovia* in Bohemia in the Katian (Havlíček, 1977). The earliest known *Eostropheodonta* was reported from lower Katian of Morocco (Havlíček, 1971). The *Aegiromena* clade is recorded in the Mediterranean Region in pre–Hirnantian, although its earliest known species occurred in Ireland during the Darriwilian (Havlíček, 1967).

Meanwhile, the *Hirnantia* Fauna also contains a variety of immigrants derived from low latitudes (Rong and Harper, 1988). For example, phylogenetically, *Paromalomena* was stem from a clade related to glyptomenids that originated in North America in early Late Ordovician; *P. macmahoni* (Reed) (=*P. polonica* Temple) has not been found in high latitudes. Similarly, the other common taxa have a low–middle latitude distribution; e.g., *Dalmanella* and *Leptaena* originated in Avalonia and Baltica, respectively in the Middle Ordovician (Rong and Cocks, 1994; Harper, 2000); and *Fardenia* and *Cliftonia* from Avalonia in Katian (Wright, 1968; Cocks, 2008). The earliest known species of *Hindella* is potentially *H. prima* from Katian of central Iran (Popov *et al.* 2015), residing probably in temperate latitudes on peri–Gondwanan terranes. These forms adapted to a wide range of conditions in the crisis, which significantly increased their probability of survival (Harper and Rong, 1995). The

rhynchonellide *Plectothyrella* was assigned to the Ancistrorhynchidae (Rong *et al.*, 2008b), but its origin remains unresolved.

Ten genera in the *Hirnantia* Fauna known from four to seven geographical units, can be divided into two groups: a few newly evolved genera may have originated from an earlier stock in the Mediterranean Region in the Katian, e.g., *Mirorthis* (Havlíček, 1977); ancestors of some taxa stem from low–mid latitudes, e.g., *Orbiculoidea*, *Triplesia*, *Pseudopholidops* and *Xenocrania*; *Pseudopholidops* appeared in the typical *Hirnantia* Fauna in Bohemia for the first time (Mergl, 1986). Besides, nearly 60 rarer genera known from one, two or three localities are thought to be from a variety of clades rooted in different regions of the world.

When the climate cooled down substantially in the early–middle Hirnantian, those ubiquitous taxa that had wide tolerance ranges, associated with some warmer water forms, joined the taxa rooted in the Mediterranean Region to constitute the *Hirnantia* Fauna worldwide. Whereas those endemic and/or rare taxa, having more specific requirements, could only adapt with difficulty to harsher conditions, and rarely joined the core of the fauna.

7.2.3 Elimination of the Hirnantia *Fauna*

Brachiopods in the early–middle Hirnantian shelly faunas are usually predominant in abundance and diversity (Harper and Hints, 2016 and therein), and often occupied about 2/3–4/5, even over 90% of the entire reported association. For example, in three succeeding collections of the *Hirnantia* Fauna at Miaoquan, Chongqing, South China, brachiopod specimens account for about 80% of the total (Fig. 22). Trilobites (*Mucronaspis* Fauna), associated with the brachiopods, the two dominant assemblages in the benthos occupied a very large vacuum of ecological spaces in level-bottom settings globally. As

rapid deglaciation brought a dramatic rise in global sea level associated with widespread anoxia in the late Hirnantian, the *Hirnantia* Fauna went extinct, and the once-flourishing trilobites were also affected, never again to recover the abundance they enjoyed in the Cambrian and Ordovician (Owen *et al.*, 1991; Zhou *et al.*, 2004, 2011). New biota (e.g., the shallow water Edgewood-Cathay Fauna) took over the eco-spaces left empty by the extinction of the *Hirnantia–Mucronaspis* Fauna. Clearly, these biological events marked the second Hirnantian phase of the end-Ordovician mass extinctions (Brenchley, 1989; Brenchley *et al.*, 2003; Harper and Rong, 1995; Rong and Harper, 1995; Sheehan, 2001; Rong *et al.*, 2002; Benedetto *et al.*, 2013; Rasmussen, 2014; Finnegan *et al.*, 2016; Huang *et al.*, 2020c). A more traditional double pulsed Hirnantian extinction model, rather than a single pulse (for South China in Hallam and Wignall, 1997; Wang *et al.*, 2019) is supported by the new dataset presented herein.

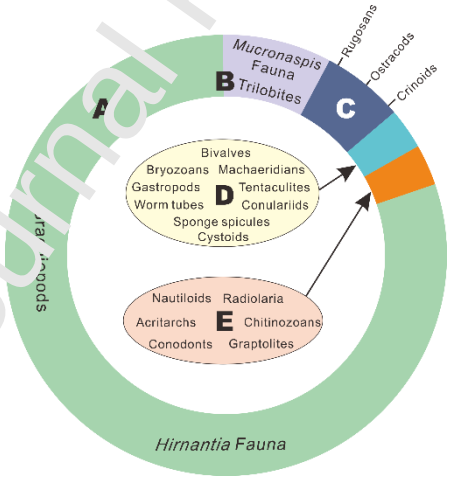

Fig. 22. Schematic diagram showing the roughly relative abundance and richness of various fossil groups in early–middle Hirnantian, shallow-water, marine environments based on the data from a number of localities in South China, Baltica (Temple, 1965; Bergström, 1968; Cocks, 1982; Hints and Harper, 2015), Laurentia (Lespérance and Sheehan, 1976), Perunica (Marek and Havlíček, 1967), Precordillera (Benedetto and Sánchez, 1990), and Sibumasu (Cocks and Fortey, 1997, 2003; Rong *et*

al., 2020; Huang *et al.*, 2020a). A. Usually predominant; B. Widespread, low diversity, locally abundant; C. Rarely highly diversified (e.g., rugosans), or highly abundant (e.g., crinoids); D. Rare, a few taxa with low abundance (e.g., machaeridians); E. Nektonic and planktonic, low diversity, usually rare.

The situation for other clades may have been different from that of brachiopods and trilobites during the crisis interval. The graptolites in the second phase experienced a minor extinction (Chen *et al.*, 2004). But, there was a significant evolutionary changeover within the major graptolite clades in late Hirnantian (Melchin *et al.*, 2011; Bapst *et al.*, 2012). For conodonts, a transformative stage from *Amorphognathus ordovicicus* to *Ozarkodina hassi* occurred within the later Hirnantian (Bergström *et al.*, 2012b), but this transition requires further investigation. The flourishing of deep-water sponges (mainly BA 5, even BA 6) occurring in the basal Lungmachi Formation (upper Hirnantian–early Rhuddanian) is stratigraphically higher than the Kuanyinchiao Bed yielding the *Hirnantia* Fauna in South China (Li *et al.*, 2015; Bo ing *et al.*, 2017, 2018). These are broadly consistent with the initial resurgence of many warm-water animals, e.g., reefs, and massive tabulates (Fig. 23), associated with pentameride and atrypide brachiopods in the late Hirnantian.

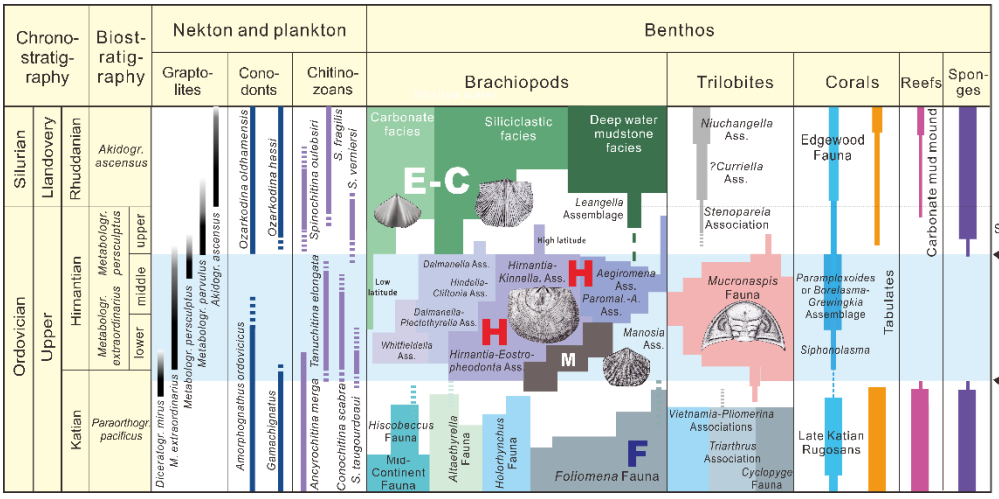

Fig. 23. Faunal succession of brachiopods, trilobites, corals, reefs, and sponges through the Ordovician and Silurian transition. E-C Edgewood-Cathay Fauna; F. *Foliomena* Fauna; H. *Hirnantia* Fauna; M. *Manosia* Community (Figure based on Amsden and Barrick, 1986; Owen *et al*., 1991; Paris *et al*., 2000; Jin and Chatterton, 1997; Jin, 2001; Copper, 2001; Koren *et al*., 2003; Chen *et al*., 2005; Stott and Jin, 2007; Elias *et al*., 2013; Vandenbroucke *et al*. 2008, 2009; Bergström *et al*., 2012a, b; Melchin *et al*., 2013; Demski *et al*., 2015; Harper and Hints, 2016; Wang *et al*., 2016, 2018; Wei and Zhan, 2017; Botting *et al*., 2017, 2018; Štorch *et al*., 2019).

7.2.4 Rise of the Edgewood-Cathay Fauna

The Edgewood-Cathay Fauna, as a whole appeared on a rather broad belt around the then equator, immediately following the second wave of the end-Ordovician crisis. However, there are two exceptions from the earlier Hirnantian, i.e., carbonate rocks yielding rare elements (e.g., *Thebesia*) in Kolyma (Koren and Sobolevskaya, 2008), and siliciclastic facies with some genera (e.g., *Brevilamnulella* and *Eospirigerina*) in Zhejiang, South China (Rong *et al*., 2013). These may have been pioneer representatives of the Fauna (Fig. 23). For the great majority, the Fauna ranges from late Hirnantian to Rhuddanian (Huang *et al*., 2019), in good agreement with the substantial rise in temperature and sea-level. Our analysis suggests that the post-glaciation faunas may have also occurred in deeper water regimes (BA 4−5, even BA 6) (Rong *et al*., 2008a; Baarli, 2019; Botting *et al*., 2019) in the late Hirnantian, when global anoxic conditions (black graptolitic shale) spread out across many places in the world, and shelly benthic faunas are extremely rare.

7.3 Speciation in the Hirnantian

As a general rule, there is a higher rate of taxonomic evolution during times of provincialism than during times of cosmopolitanism (Boucot, 1975). The Hirnantian, however, may be an exception marking the end of a prolonged interval of dispersion. The Hirnantian provincialism through the O−S transition was weak, yet the evolution of the brachiopods was rapid, perhaps against a background of extreme climate change.Our dataset reveals many newly-established genera within the Hirnantian, possibly seeding the recovery of the benthos prior to the Silurian This unusual evolutionary rate seems to be rare in other macro-faunas in the Hirnantian (Harper and Rong, 1995). Within the brachiopods, at least, high originations of new taxa may be linked to intervals of accelerated speciation due to extreme climatic conditions (Rasmussen *et al.*, 2019).

7.3.1 The Hirnantia *Fauna*

This fauna includes 21 new genera accounting for 25% of the whole fauna, including orthides (11 genera), strophomenides (4), and rhynchonellides (3) (Fig. 24). Some (e.g., *Kinnella* and *Paraomalomena*) have wide distributions; the others (e.g., *Dysprosorthis* and *Toxorthis*) are recorded in more limited regions. Endemic taxa are mostly from the Kosov Province (e.g., *Titanomena* in Sweden, and *Minutomena* in South China and Sibumasu). The strophodontids may have originated from *Eostropheodonta* in early–middle Hirnantian, as a species with denticular plates but lacking dental plates has been identified as '*Palaeoleptostrophia*' in Sibumasu (Rong *et al.*, 2020) and South China (Huang *et al.*, 2020a, b), and probably as leptostrophiids in East Baltica (Harper and Hints, 2016).

7.3.2 The Edgewood-Cathay Fauna

There are 19 new genera known to comprise about 1/4 of the Edgewood-Cathay Fauna. They were not spread across all the taxonomic groups; seven from orthides, five from rhynchonellides, and three from atrypides, lacking the pentamerides. The latter group was suppressed, and did not recover until the late Rhuddanian (Harper and Rong, 1995; Jin and Copper, 2000, 2010; Jin *et al*., 2007; Cocks and Rong, 2008; Huang *et al.*, 2012, 2018).

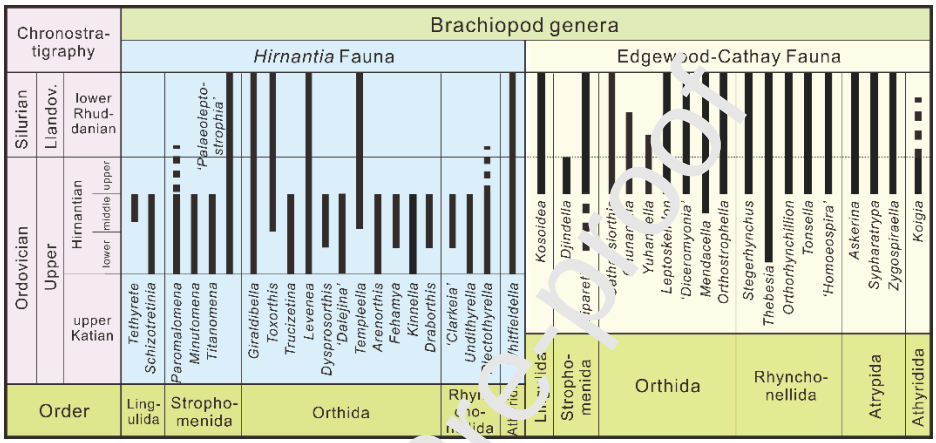

Fig. 24. Origination of newly-established genera in the *Hirnantia* Fauna and the Edgewood-Cathay Fauna, with their ordinal assignments during the Ordovician and Silurian transition.

In short, the origination of brachiopods in the two survival intervals is represented only by genera and species, but not by any new higher rank taxa. Although the taxonomic compositions of newly-evolved genera in the two faunas are substantially different, the percentages are similar. The highest origination rates in the *Hirnantia* Fauna occurred within the orthides and strophomenides, suggesting their continued resilience in early–middle Hirnantian diversifications of these orders. With the exception of the orthides, however, the rhynchonellides and atrypides have higher rates in the Edgewood-Cathay Fauna, indicating that these two groups embraced more chances for survival than pentamerides and others. During the late Hirnantian, brachiopod speciation may have been a response to crises, which increased the rate of phyletic evolution, particularly in South China, which may have

acted as a cradle of evolution at that time.

7.4 Where were Lazarus taxa during the crisis interval?

During the crisis, high environmental pressures strongly influenced global biodiversity. There are many taxa recognized as Lazarus taxa *sensu stricto* (Flessa and Jablonski, 1983) that were recorded from older Ordovician rocks and survived the crisis in yet undiscovered refugia (Harper and Rong, 1995; Rong *et al.*, 2006; Rasmussen *et al.*, 2011b; Huang *et al.*, 2014). Where they all hid during the crisis is a mystery. Rasmussen and Harper (2011b), however, in a detailed global analysis of the distribution of brachiopods through the crisis, suggested that Baltica may be viewed as a shallow-water refuge during the crisis together with other shallow-water refuges such as Gondwana, Kazakhstan and the peri-Laurentian terranes. South China, in particular, seems to have been a good habitat for the mid-deep shelf faunas.

The Lazarus taxa can be regarded as extreme examples of declining taxa (Rong *et al.*, 2006) at various systematic levels, e.g., genus (*Holorhynchus*), family (Strophochonetidae), superfamily (Camerelloidea), and order (Trimerellida). The declining taxa shared common characters, including low abundance, small population size, and scattered, in some cases isolated, geographic distributions with a very much reduced presence in the early–middle Hirnantian, such as *Skenidioides* in Myanmar (Rong *et al.*, 2020), West Yunnan (Huang *et al.*, 2020a, c) and Maine; *Epitomyonia* and *Leangella* in Maine; and the latter from Estonia (Hints and Harper, 2015) and France (Álvaro *et al.*, 2016) (Fig. 25). These forms occupied BA 4–5 mostly in low latitudes in pre-Hirnantian Ordovician; but invaded better oxygenated, shallower water environments in lower temperatures, a regime favored by the *Hirnantia*

Fauna. It indicates that migration from deep-water to shallower water settings favored survival to avoid deteriorating environments that led to the demise of the *Foliomena* Fauna. The record of shallow water facies during Hirnantian regression is markedly incomplete and biased towards more marginal/deeper water facies, requiring a much greater focus on shallow water, intra-cratonic deposits, particularly in low latitudes. The Lazarus taxa, e.g., trimerellides could not adapt to cold/cool environments and may have hid in relatively warmer and ventilated water regimes during the end-Ordovician crisis.

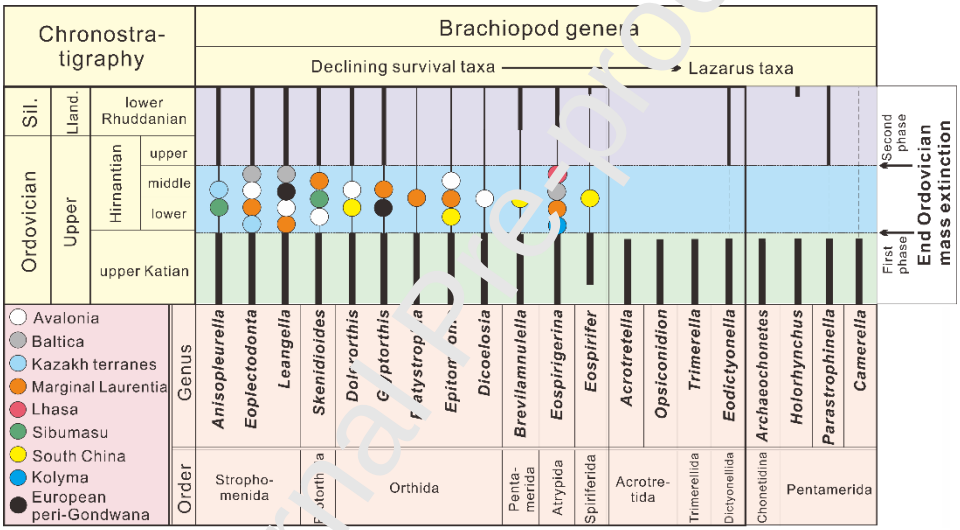

Fig. 25. Geographical occurrences of selected declining genera in the early–middle Hirnantian, when Lazarus taxa were unknown in terms of current fossil records. Our study indicates that the Lazarus taxa may have retreated to both shallow and deeper-water regimes in the then low latitudes (See also Rasmussen and Harper, 2011b).

7.5 Causes and consequences: abiotic and biotic complexity

Our investigation confirms that environmental changes on a global scale during the end-Ordovician crisis were more complex than hitherto envisaged. The complexity is manifested by

both external and biological factors. The main abiotic factors included substantial climate change (e.g., Finnegan *et al.*, 2011; Algeo *et al*., 2016), sea-level fluctuations (e.g., Brenchley *et al.*, 2006), changes in ocean chemistry and circulation (e.g., Berry and Wilde, 1978; Sheehan, 2001), atmospheric carbon and oxygen perturbations (e.g., Brenchley *et al.*, 1994; Kaljo *et al.*, 2008; Bergström *et al*., 2014 and therein), intense orogenic movements (Rasmussen and Harper, 2011a) and volcanic activity (McKenzie *et al*., 2016; Jones *et al*., 2017; Gong *et al*., 2017; Bond and Grasby, 2020), within a very short duration (e.g., Brenchley *et al.*, 1994; Ling *et al.*, 2019). The biological responses to these factors are largely characterized by taxonomic extinctions, phyletic origination, faunal turnovers, and changes in community structure. Harper *et al*. (2014) pointed out that the end-Ordovician mass extinctions were a product of the coincidence of a number of contributing factors.

There are different opinions regarding the magnitude of temperature changes during the formation of the major glaciation, varying from ~4°C (Trotter *et al*., 2008), 5–6°C (Finnegan *et al.*, 2011), ~10°C (Brenchley *et al.*, 2003), to even up to ~14°C (Pohl *et al.*, 2016; see Rasmussen *et al.* 2019 for compilation of temperature data), nevertheless the change was sufficiently substantial to cause biotic extinction. During the glaciation, marine temperature differences existed between the poles and the equator (Sheehan, 2001), and such gradients were uneven across latitudes and water depths as global cooling was heterogeneous. Low latitudes cooled more than high latitudes, and thus the temperature may have fluctuated more in lower latitudes and shallower water settings than in higher latitudes and deeper water (Finnegan *et al.*, 2016). Even though the rate and the trend of climate changes in latest Ordovician and present are not the same, it would still be feasible to presume the heterogeneity in Ordovician based on the principle of uniformitarianism. Such heterogeneous change of seawater temperature across latitudes and water depths had a significant impact on the *Hirnantia* Fauna

(Finnegan *et al.*, 2016). The sea-level fluctuation induced by global climate change eventually caused the changes of *Hirnantia* Fauna in composition, diversity, and community succession.

The complexity is also reflected in the nature of the two-phased extinction. Based on our study, each of the two phases was not an abrupt and simultaneous event on a global scale, but was a process of transition within a very short geological interval. It may vary in different palaeogeographic locations. According to the earlier discussion, the emergence of the *Hirnantia* Fauna is diachronous, suggesting that the cold-water environments induced by glaciation started in different places at different times. There were also temporal and spatial differences at the termination of the major glaciation, which is recognized by different communities of the Fauna laterally and vertically. For example, some carbonate factories occur in a gradual shallowing upwards Hirnantian succession (from BA3 to BA2) in near-shore settings, as manifested by the *Dalmanella–Plectothyrella* Community in northern Guizhou (Rong and Li, 1999) and Estonia–Latvia (Harper and Hints, 2016) (Fig. 7). Whereas other siliciclastic facies are marked by the *Anisopleurella–Aegiromena* Community in an off-shore, deepening upwards Hirnantian succession (from BA3 to BA4) in southwestern Yunnan (Huang *et al.*, 2020c). The two communities are interpreted to occur in the interval of transition from the later to latest stage of the glaciation and the start of global sea-level rise.

The timing and intensity of the effects of environmental upheavals vary from place to place, reflecting this complexity. Immediately following the middle Hirnantian, major Gondwanan glaciation ceased, the climate started to ameliorate, along with global anoxia induced by the dramatic sea-level rise (e.g., 80–100 m, Brenchley *et al.*, 2006), and oceanic circulation stagnated. Global flooding by anoxic waters has been commonly considered the cause of the second phase of the crisis (Hammarlund *et al*., 2012; Bartlett *et al*., 2018; Zou *et al*., 2018; Stockey *et al*., 2020). Our study demonstrates that in

many continuous stratigraphic successions across the Ordovian–Silurian boundary, the *Hirnantia* Fauna–bearing beds are is overlain by upper Hirnantian–lowest Rhuddanian black shale, indicating the onset of a global transgressive event. Anoxia was prevalent and diachronous across different sites, latitudes, facies, and depths mostly within the middle–upper *M. persculptus* Biozone. As a result, in shallow-water settings (BA 2–3) where the anoxic conditions were absent, the *Hirnantia* Fauna was replaced by the Edgewood-Cathay Fauna (BA 2–3); a few survived the crisis for example the oxygen-depleted, deep-water biota from Baltica (Baarli and Harper, 1982) and Avalonia (Harper and Williams, 2002); the others (e.g., pentamerides and atrypides) that colonized warm water environments survived the global perturbations, and became the backbone of the Silurian fauna (Fig. 26).

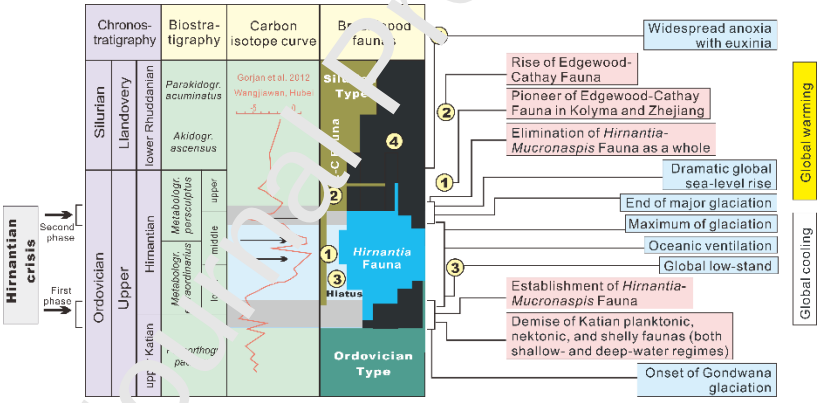

Fig. 26. Carbon isotope excursions, brachiopod faunas together with the position of the major glaciation, and other key biotic and oceanic events through the Ordovician and Silurian transition (Sheehan, 2001; Finnegan *et al.*, 2011; Gorjan *et al.*, 2012; Rasmussen *et al.*, 2011b among others).

The complexity of a range of interwoven factors constituting a chain of events, has presented difficulties for precise global correlation of the strata through the multi-causal catastrophe (Harper *et al.*, 2014), which has generated some debatable carbon isotope curves recorded within the Hirnantian

Stage (e.g., Kump *et al.*, 1999; Kaljo *et al.*, 2008; LaPorte *et al.*, 2009; Gorjan *et al.*, 2012; Bergström and Goldman, 2019). The records of the carbon isotope excursions through Hirnantian vary substantially across sites not only in the precise timing of the peak or minimum values, but also in the magnitude of the excursions and the duration of the events (Fig. 26). Further investigation of the Hirnantian chemostratigraphy is needed, particularly where curves are utilized for precise stratigraphic correlation.

The 'Big Five Extinctions' have many characteristics in common, e.g., a dramatic loss of biodiversity (magnitude), related to a wide range of biota (breadth), over a short time interval (duration), and worldwide (extent) (Sepkoski, 1981; Raup and Sepkoski, 1982). However, each mass extinction has its own unique characteristics; each is at a different stage of biological evolution, and has different triggers with diverse consequences, durations, and associations with patterns of environmental perturbations. The unique nature of the threat to the Earth's biodiversity is not simply due to the magnitude of each driver, but due to many factors, such as the velocity of change, the novelty of the drivers, and their interactions (Sage, 2020). A considerable wealth of data from Hirnantian brachiopods confirm that there were two phases of the extinction corresponding to the start and end of the main phase of the Late Ordovician glaciation (Brenchley *et al.*, 1994, 2006; Harper and Hints, 2016). Major changes in marine eco-habitats occurred twice during the Hirnantian (the first and second pulses) and taxa disappeared or lost their dominant roles and with the subsequent replacement by new faunas. It indicates that intense climate change, sea-level fall and a subsequent sharp rise, and oceanographic ventilation and anoxia, had important roles in brachiopod evolution through the crisis, as taxa adapted to first cool and then warm water conditions. Other factors, such as plate tectonics (Rasmussen and Harper, 2011a) may have also caused complex and influential environmental perturbations. Moreover,

the distinctive characters of the survival and recovery aftermath at the end of the Ordovician, make it unique amongst the 'Big Five Extinctions'.

8. Concluding remarks

This review clarifies a number of key issues and identifies some new challenges. Based on a newly compiled, comprehensive database, quantitative and qualitative analyses have helped to recognize the characteristics of the Hirnantian brachiopod faunas and their spatial distributions and temporal succession. A biostratigraphic correlation chart is provided for a better understanding of the global changes across the Ordovician–Silurian transition mostly based on graptolites, condonts, chitinozoans and brachiopods.

1. The *Hirnantia* Fauna is a conflation of a large variety of genera, derived from not only the cold regions, but also from the tropics, with different geographic and phylogenetic origins, assembled during the early–middle Hirnantian from *M. extraordinarius* to lower *M. persculptus* biozones, when climatic and oceanic conditions dramatically changed.

2. The *Hirnantia* Fauna adapted to cool/cold water environments in different depths on various types of substrates in most parts of the globe, ranging from the southern hemisphere to many, but not all parts, of northern hemisphere. The latter areas are typified by shallow water carbonate facies and may have not been reached by oceanic currents bearing the larvae of the taxa of the Fauna.

3. The *Hirnantia* Fauna possesses rare occurrences of pentamerides and atrypides. These forms responded well to warmer climatic conditions in the tropics and established their dominance during the Silurian and Devonian. Interestingly, these two groups plus the strophodontids became extinct during

the Late Devonian F/F mass extinction.

4. During the glaciation, the environmental change was very complex. Well-constrained associations of the *Hirnantia* Fauna may indicate that the marine temperature gradient did exist along latitude and water depth. Near-shore carbonate factories in a shallowing upward succession, and off-shore siliciclastic facies in a deepening upward succession may have been resulted from the late stage of the glaciation, and the start of glacial melting, respectively within the mid Hirnantian.

5. After the glaciation, the *Hirnantia* Fauna was replaced by yet another fauna, better adapted to warmer water, the Edgewood-Cathay Fauna, a successor characterized by high diversities of major taxa on carbonate and/or siliciclastic substrates, which contained the roots of the Silurian brachiopod faunas. The development is in accordance with the presence of tabulates, reefs, stromatoporoids, and many other typical warm water organisms (e.g., pentamerides and atrypides) following the end of the glaciation.

6. There occurred two phases based on robust data mainly from the two predominant and common elements of the benthos, the brachiopods and trilobites. The acme of the *Hirnantia–Mucronaspis* Fauna, as a whole, was linked to the major Gondwana glaciation, and the emergence of the Edgewood-Cathay Fauna replacing the *Hirnantia* Fauna is considered as the product of a post-glacial world. Importantly, each phase was not abrupt and instantaneous, but rather a very complex process within a short geological time interval. This mass extinction is expressed not only by magnitude of biodiversity loss, but essentially by ecosystem destruction and faunal turnover.

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Declaration of interest:

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix I

A. The *Hirnantia* Fauna (H1–H89)

H1, Lower part of the Lower Second Bani Member, Anti-Atlas, Morocco: *Hirnantia*, *Destobesium*, *Eostropheodonta* (Colmenar *et al.*, 2015, 2019)

H2, Upper part of the Lower Second Bani Member, Anti-Atlas, Morocco: '*Dalejina*', *Hirnantia*,

Destobesium, *Eostropheodonta*, '*Resserella*', *Clarkeia*, *Mirorths* (=their *Horderleyella*), *Arenorthis*, *Kinnella*, *Fehamya*, *Plectothyrella* (more taxa, indeterminate) (Villas *et al.*, 2016; Colmenar *et al.*, 2015, 2019)

H3, Alnif Member of Upper Second Bani Member, Anti-Atlas, Morocco: *Destombesium* (Colmenar and Álvaro, 2015)

H4, Tamekhtart Member of Upper Second Bani Member, Anti-Atlas, Morocco: *Arenorthis*, *Destobesium*, *Eostropheodonta* (Villas *et al.*, 2006; Colmenar *et al.*, 2015, 2019)

H5, Amouktir Member of Upper Second Bani Member, Anti-Atlas, Morocco: *Hirnantia Eostropheodonta*, *Destobesium*, *Kinnella*, *Plectothyrella*, *Undithyrella* (Colmenar and Álvaro, 2015; Colmenar *et al.*, 2015, 2019)

H6, Coastal Meseta, Northern Morocco: *Arenorthis* (Sutcliffe *et al.*, 2001)

H7, Algeria: *Arenorthis*, *Eostropheodonta*, *Hindella*, *Hirnantia* (Mergl, 1983; Popov *et al*., 2019).

H8, Libya: *Eostropheodonta*, *Hirnantia*, *Plectothyrella* (Havlíček and Massa, 1973; Sutcliffe *et al.*, 2001).

H9, Zhusilenghaierhan, Inner Mongolia: *Cliftonia*, *Dalmanella*, *Leptaena*, *Triplesia* (Rong *et al*., 2003).

H10, Hol Beck, Westmorland, N England: *Dalmanella*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Lingulella*, *Paromalomena*, *Plectothyrella*, *Xenocrania* (Temple, 1965; Chen and Rong, 2019).

H11, Keisley, N England: *Aegiromena*, *Dicoelosia*, *Dolerorthis*, *Draborthis*, *Dysprosorthis*, *Fardenia*, *Hindella*, *Hirnantia*, *Onychoplecia*, *Paracraniops*, *Paromalomena*, *Petrocrania*, *Pionodema*, *Pseudopholidops*, *Skenidioides*, *Salopina*, *Sphenotreta*, *Templeella*, *Toxorthis*, *Xenocrania* (Temple, 1968; Chen and Rong, 2019).

H12, Arber Hirnant, N Wales: *Dalmanella*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Mirorthis*, *Plectothyrella* (Temple, 1965).

H13, Hirnant Quarry, Arber Hirnant, N Wales: *Dalmanella*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Mirorthis*, *Plectothyrella*, *Skenidioides* (Cocks and Price, 1975).

H14, Berwyns, N Wales: *Paromalomena*, *Hirnantia*, *Eostropheodonta*, *Hindella*, *Dalmanella*, *Kinnella*, *Plectothyrella*, *Sowerbyella*?, *Mirorthis*, *Rhynchotrema*?, *Plaesiomys*, *Epitomyonia* (Brenchley and Cullen, 1984).

H15, Meifod, Central Wales: *Hindella*, *Hirnantia*, *Eostropheodonta*, *Dalmanella*, *Rhynchotrema*?, *Kinnella*, *Leangella*, *Paromalomena*, *Plectothyrella* (Brenchley and Cullen, 1984; Brenchley *et al*., 2006).

H16, Haverfodwest, SW Wales: *Chonetoidea*, *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Giraldibella*, *Hindella*, *Hirnantia*, *Leptaena*, *Pseudolingula*?, *Orbiculoidea*, *Paracraniops* (=their *Craniops*), *Philhedra*, *Skenidioides* (Cocks and Price, 1975).

H17, A_1 Llandovery, SW Wales: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Giraldibella*, *Hindella*, *Hirnantia*, *Leptaena*, *Plectatrypa*, *Skenidioides* (Williams, 1951).

H18, Kildare, Ireland: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Leptaena*, *Plectothyrella* (Wright, 1968).

H19, Västergötland, Sweden (Locality 2): *Cliftonia*, *Dalmanella*, *Draborthis*, *Drabovia*, *Eostropheodonta*, *Giraldibella*, *Hirnantia*, *Horderleyella*, *Kinnella*, *Leptaena*, *Orbiculoidea*, *Pseudopholidops*, *Plectothyrella*, *Titanomena*, *Xenocrania* (Bergström, 1968; Chen and Rong, 2019).

H20, Västergötland, Sweden (Locality 5): *Cliftonia*, *Dalmanella*, *Draborthis*, *Drabovia*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hirnantia*, *Horderleyella*, *Kinnella*, *Leptaena*, *Orbiculoidea*, *Petrocrania*, *Plectothyrella*, *Titanomena* (Bergström, 1968).

H21, Västergötland, Sweden (Locality 13): *Cliftonia*, *Dalmanella*, *Draborthis*, *Drabovia*, *Eostropheodonta*, *Fardenia*, *Hirnantia*, *Horderleyella*, *Leptaena*, *Plectothyrella* (Bergström, 1968).

H22, Edefors, Jämtland, Sweden: *Aegiromena* (Dahlqvist *et al*., 2010).

H23, Nifsåsen, Jämtland, Sweden: *Aegiromena*, *Dysprosorthis*, *Leptaena* (Dahlqvist *et al*., 2010).

H24, Rannåsen, Jämtland, Sweden: *Dalmanella*, *Dysprosorthis*, *Eostropheodonta*, *Kinnella*, *Leptaena*, *Orbiculoidea* (Dahlqvist *et al*., 2010).

H25, Oslo-Asker, Norway (e.g., locality: 18, 107, 109): *Hirnantia*, *Dalmanella*, *Eostropheodonta*, *Cliftonia*, *Hindella* (*Hirnantia* Association: Brenchley and Cocks, 1982)

H26, Oslo-Asker, Norway (e.g., locality: 9, 30, 33): *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Hindella* (Cocks, 1982; *Hindella-Cliftonia* Association: Brenchley and Cocks, 1982)

H27, Oslo-Asker, Norway (e.g., locality: 34, 41): *Dalmanella*, *Cliftonia*, *Hindella*, *Hirnantia* (Cocks, 1982; *Dalmanella* Association: Brenchley and Cocks, 1982; Brenchley and Cullen, 1984)

H28, Ruhnu, Estonia: *Cliftonia*, *Dalmanella*, *Draborthis*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Leptaena*, *'Palaeoleptostrophia'*, *Paromalomena*, *Plectothyrella* (Hints *et al*., 2012; Harper and Hints, 2016).

H29, Ikla, Estonia: *Cliftonia*, *Dalmanella*, *Eoplectodonta*, *Eospirigerina*, *Eostropheodonta*, *Hindella*, *Leptaena*, *Paromalomena*, *Plectothyrella*, *Trematis* (Hints *et al*., 2012, 2015; Harper and Hints, 2016).

H30, Taagepera, Estonia: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *'Palaeoleptostrophia'*, *Plectothyrella* (Hints *et al*., 2012, 2015; Harper and Hints, 2016).

H31, Aispute 41, Latvia: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *'Palaeoleptostrophia'*, *Paromalomena*, *Plectothyrella* (Hints *et al*., 2012, 2015; Harper and Hints, 2016).

H32, Mezmali-16, Latvia: *Cliftonia*, *Dalmanella*, *Draborthis*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Leptaena*, *Onniella*, *'Palaeoleptostrophia'*, *Paromalomena*, *Plectothyrella* (Hints *et al*., 2012, 2015; Harper and Hints, 2016).

H33, Stawy, Holy Cross Mountains, S Poland: *Dalmanella*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Lingulella*, *Mirorthis*, *Orbiculoidea*, *Paromalomena*, *Plectothyrella*, *Xenocrania* (Temple, 1965; Chen and Rong, 2019).

H34, Western Armorica, N France: *Hirnantia*, *Plectothyrella*? (Mélou, 1987)

H35, Association 1, Villerouge-Termenès, Mouthoumet, S France: *Hindella*, *Plectothyrella* (Álvaro *et al*., 2016).

H36, Associations 2–4, Villerouge-Termenès, Mouthoumet, S France: *Eostropheodonta*, *Glyptorthis*, *Leangella*, *Leptaena*, *Orbiculoidea*, *Paucicrura*, *Plectothyrella*, *Rostricellula* (Álvaro *et al*., 2016).

H37, Association 5, Gascagne, Mouthoumet, S France: *Dalmanella*, *Destobesium*, *Drabovinella*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Howellites*, *Kinnella*, *Leangella*, *Leptaena*, *Plectothyrella* (Álvaro *et al*., 2016).

H38, Carnic Alps: *Clarkeia*, *Dalmanella*, *Hindella*, *Hirnantia*, *Kinnella*, *Paromalomena* (Jaeger *et al*., 1975; Schönlaub *et al*., 2011).

H39, Sardinia, Italy: *Dalmanella*, *Hirnantia*, *Kinnella*, *Mirorthis*, *Plectothyrella* (Leone *et al*., 1991).

H40, Argovejo, Cantabrian Zone, NW Spain: *Cliftonia*, *Draborthis*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Leptaena*, *Orbiculoidea*, *Plectothyrella* (Bernárdez *et al*., 2014).

H41, Valdeteja, Cantabrian Zone, NW Spain: *Arenorthis*, *Eostropheodonta*, *Plectothyrella* (Bernárdez *et al*., 2014).

H42, Cerveruela, Asturian-Leonese Zone, Spain: *Eostropheodonta*, *Plectothyrella* (Bernárdez *et al*., 2014).

H43, Almadén, Central Iberian Zone, south-central Spain: *Hirnantia*, *Kinnella*, *Plectothyrella* (Villas *et al*., 1999; Bernárdez *et al*., 2014).

H44, Central Portugal: *Mirorthis*, *Paromalomena*, *Paracraniops*? (=their Discinidae gen. *et* sp. indet.), *Plectoglossa*?, *Plectothyrella* (Colmenar *et al*., 2012).

H45, No. 264, Zhigeli River, Durben, Chu-Ili: *Paromalomena* (Nikitin *et al*., 1980).

H46, No. 286, Ojsu Creek, Chu-Ili: *Cliftonia*, *Dalmanella*, *Eoplectodonta*, *Fardenia*, *Giraldibella*, *Leptaena*, *Orbiculoidea*, *Rhynchotrema*, *Rugosowerbyella*, *Streptis*, *Templeella*, *Triplesia* (Nikitin *et al*., 1980).

H47, No. 287/94, Krylo North, Chu-Ili: *Aegiromena*, *Anisopleurella*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Hirnantia*, *Leptaena*, *Paromalomena* (Nikitin *et al*., 1980).

H48, No. 276-279, Krylo South, Chu-Ili: *Paromalomena*, *Eostropheodonta*, *Aegiromena*, *Dalmanella* (Nikitin *et al*., 1980).

H49, Québec, E Canada: *Dalmanella*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Plectothyrella* (Lespérance and Sheehan, 1976).

H50, Zhiwazuogu section (ADG 46), Xainza, Central Xizang: *Cliftonia*, *Dalmanella*, *Eospirigerina*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Paromalomena* (Rong and Xu, 1987).

H51, Zhiwazuogu section (ADG 47), Xainza, Central Xizang: *Cliftonia*, *Dalmanella*, *Dysprosorthis*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Leptaena*, *Paromalomena*, *Plectothyrella* (Rong and Xu, 1987).

H52, Riajue section (ADG 24), Xainza, Central Xizang: *Aegiromena*, *Cliftonia*, *Dalmanella*, *Dysprosorthis*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Paromalomena* (Rong and Xu, 1987).

H53, Girvan, S Scotland 1: *Eochonetes*, *Eostropheodonta*, *Fardenia*, *Hindella* (Harper, 1981, 2006).

H54, Girvan, S Scotland 2: *Eochonetes*, *Eopholidostrophia*, *Eospirigerina*, *Eostropheodonta*, *Fardenia*, *Glyptorthis*, *Hindella*, *Hirnantia*, *Hypsiptycha*, *Plaesiomys*, *Platystrophia*, *Rostricellula* (Harper, 1981, 2006).

H55*, Maine, USA (Locality A): *Cliftonia*, *Dalmanella*, *Eoplectodonta*, *Eostropheodonta*, *Epitomyonia*, *Hindella*, *Hirnantia*, *Kinnella*, *Leangella*, *Leptaena*, *Plectothyrella*, *Skenidioides* (This paper).

H56*, Maine, USA (Locality B): *Cliftonia*, *Dalmanella*, *Eoplectodonta*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Kinnella*, *Plectothyrella*, *Trucizetina* (This paper).

H57*, Maine, USA (Locality C): *Aegiromena*, *Christiania*, *Cliftonia*, *Dalmanella*, *Draborthis*, *Eostropheodonta*, *Fardenia*, *Hirnantia*, *Kinnella*, *Leptaena*, *Philhedra*, *Plectothyrella*, *Toxorthis* (This paper).

H58*, Maine, USA (Locality D): *Dalmanella*, *Eoplectodonta*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Kinnella*, *Plectothyrella* (This paper).

H59, New Zealand: *Cliftonia*, *Eostropheodonta*, *Hindella*, *Leptaena*, *Plectothyrella* (Cocks and Cooper, 2004).

H60, Uppermost Kosov Formation, Bohemia: *Aegiromena*, *Cliftonia*, *Comatopoma*, *Dalmanella*, *Draborthis*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Mirorthis*, *Onniella*, *Orbiculoidea*, *Paromalomena*, *Petrocrania*, *Plectothyrella*, *Pseudopholidops*, *Rafangoflossa*, *Ravozetina*, *Schizotretinia*, *Tethyrete*, *Trucizetina*, *Xenocrania* (Marek and Havlíček, 1967; Havlíček, 1967, 1977, 1989, 1994; Mergl, 1986; Chen and Rong, 2019).

H61, Basal Kosov Formation, Bohemia: *Hirnantia*, *Kinnella* (Mergl, 2011).

H62, *Hirnantia-Modiolopsis* Community, Don Braulio Section, Villicum Range, San Juan, Precodillera, Argentina: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Facifera*?, *Fardenia*, *Hirnantia*, *Paromalomena*, *Plectothyrella* (Benedetto, 1986, 1987, 1990, 2003; Sánchez *et al.*, 1991).

H63, Levels above the *Hirnantia-Modiolopsis* Community, Villicum Range, San Juan, Precodillera, Argentina: *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Leptaena*, *Plectothyrella*, *Trematis* (Sánchez *et al.*, 1991; Leone and Benedetto, 2019).

H64, Levels 4 and 5 in La Vinchuca Section, Sierra de Villicum, San Juan, Argetina: *Paromalomena*, *Eostropheodonta*, *Hirnantia*, *Dalmanella*, *Cliftonia* (Sánchez *et al.*, 1991)

H65, Cerro La Chilca, San Juan, Precodillera, Argentina: *Dalmanella*, *Drabovia*, *Paromalomena*, *Plectothyrella*, *Orbiculoidea* (Astini and Benedetto, 1992; Leone and Benedetto, 2019).

H66, Lower Shichengzi Formation, Gulang, Qilian, Gansu, NW China: *Aegiromena*, *Paromalomena* (Qu, 1986).

H67, Middle–upper part of Shichengzi Formation, Gulang, Qilian, Gansu, NW China: *Cliftonia*, *Triplesia*, *Leptaena*, *Paromalomena* (Qu, 1986).

H68, Upper Wanyaoshu Formation, Luxi, southwestern Yunnan, SW China: *Aegiromena*, *Anisopleurella*, *Cliftonia*, *Dalmanella*, *Draborthis*, *Dysprosorthis*, *Eostropheodonta*, *Giraldibella*,

Glyptorthis, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Mirorthis*, *'Palaeoleptostrophia'*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*, *Skenidioides*, *Templeella*, *Toxorthis*, *Xenocrania* (Huang *et al*., 2020a).

H69, Lower Wanyaoshu Formation, Luxi, southwestern Yunnan, SW China: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Minutomena*, *Paromalomena*, *Plectothyrella* (Huang *et al*., 2020a).

H70, Thailand: *Aegiromena*, *Cliftonia*, *Hirnantia*, *Mirorthis*, *Onniella*, *Paromalomena* (Cocks and Fortey, 1997).

H71, Northern Shan State, Myanmar: *Aegiromena*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Kinnella*, *Minutomena*, *Paromalomena*, *Pseudopholidops*, *Xenocrania* (=their *Orthisocrania*?) (Cocks and Fortey, 2002; Chen and Rong, 2019).

H72, Mandalay, Myanmar: *Aegiromena*, *Cliftonia*, *Dalmanella*, *Draborthis*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Levenea*, *Leptaena*, *Minutomena*, *Mirorthis*, *'Palaeoleptostrophia'*, *Paromalomena*, *Petrocrania*, *Plectothyrella*, *Pseudolingula*?, *Pseudopholidops*, *Skenidioides*, *Toxorthis*, *Trucizetina*, *Xenocrania* (Rong *et al*., 2020).

H73, Parana, Paraguay: *Anenorthis*, *Eostropheodonta*, *Hindella*, *Plectothyrella* (Benedetto *et al*., 2013).

H74, Subandean Range, Bolivia: *Hirnantia* (Benedetto *et al*., 1992).

H75, Yichang, western Hubei, S China: *Acanthocrania*, *Aegiromena*, *Cliftonia*, *Dalmanella*, *Draborthis*, *Dysprosorthis*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Pseudolingula*?, *Manosia*, *Minutomena*, *Mirorthis*, *Orbiculoidea*, *Onychoplecia*, *Paromalomena*, *Petrocrania*, *Plectothyrella*, *Pseudopholidops*, *Sphenotreta*, *Toxorthis*, *Triplesia*, *Trucizetina*, *Xenocrania* (Rong, 1984; Zeng *et al*., 2016; Chen and Rong, 2019; this paper).

H76, Xiushan, southeastern Chongqing, S China: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*, *Triplesia*, *Xenocrania* (This paper).

H77, Songtao, northeastern Guizhou, S China: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Paromalomena*, *Plectothyrella*, *Trucizetina* (This paper).

H78, AFA295, Honghuayuan, Tongzi, northern Guizhou, S China: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Mirorthis*, *Orbiculoidea*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*, *Trematis* (Rong *et al*., 2002; this paper).

H79, AFA306, Honghuayuan, Tongzi, northern Guizhou: *Brevilamnulella*, *Dalmanella*, *Eostropheodonta*, *Hindella*, *Hirnantia*, *Paromalomena*, *Plectothyrella* (This paper).

H80, AFA311b, Honghuayuan, Tongzi, northern Guizhou: *Dalmanella*, *Eospirifer*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Plectothyrella*, *Pseudopholidops* (This paper).

H81, Renhuai 1, northwestern Guizhou, S China: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Mirorthis*, *Orbiculoidea*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*, *Xenocrania* (Rong *et al*., 2002; this paper).

H82, Renhuai 2, northwestern Guizhou, S China: *Dalmanella*, *Fardenia*, *Eostropheodonta*, *Plectothyrella* (including their *Dorytreta*), *Hindella* (Rong *et al.*, 1999; this paper).

H83, Daguan, northeastern Yunnan, S China: *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Hirnantia*, *Kinnella*, *Leptaena*, *Orbiculoidea*, *Paromalomena*, *Plectothyrella*, *Pseudolingula*? (This paper).

H84, Changning, southern Sichuan, S China: *Aegiromena*, *Cliftonia*, *Dalmanella*, *Dolerorthis*, *Draborthis*, *Dysprosorthis*, *Eostropheodonta*, *Epitomyonia*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Leptaena*, *Mirorthis*, *Onniella*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*,

Sphenotreta, *Toxorthis*, *Triplesia*, *Xenocrania* (Rong *et al*., 2002; Chen and Rong, 2019; this paper).

H85, Nanjiang, northern Sichuan, S China: *Aegiromena*, *Cliftonia*, *Dalmanella*, *Draborthis*, *Dysprosorthis*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Hirnantia*, *Kinnella*, *Levenea*, *Leptaena*, *Orbiculoidea*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*, *Sphenotreta*, *Toxorthis*, *Triplesia*, *Trucizetina*, *Xenocrania* (This paper).

H86, Nanzheng, southern Shaanxi, S China: *Aegiromena*, *Dalmanella*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hindella*, *Hirnantia*, *Kinnella*, *Orbiculoidea*, *Paracraniops*, *Paromalomena*, *Plectothyrella*, *Pseudopholidops*, *Triplesia*, *Trucizetina*, *Xenocrania* (This paper).

H87, Wuning, northwestern Jiangxi, S China: *Aegiromena*, *Fardeina*, *Paromalomena* (This paper).

H88, Jingxian, southern Anhui, S China: *Aegiromena*, *Fardeina*, *Paromalomena* (This paper).

H89, Lin'an, northern Zhejiang, S China: *Aegiromena*, *Paromalomena* (This paper).

* H1–H5: Rare data also come from Havlíček (1971) and Villas *et al*. (2016).

**H53, H54, H55, H56: Four localities (A, B, C, D) of Maine, USA, collected by Bob Neuman and his colleagues in 1968 (with acquisition numbers: A. No. 13030, B. No. 13031, C. Pond Pitch-Haskell Rock; D. Mencher-Pudding Stone). These fossils were identified by one of the authors (J.Y. Rong) in 1987 and 1997.

B. Edgewood-*Cathaysiorthis* Fauna (E1–E30)

E1, Noix Limestone, Missouri and Ilinois, USA: *Cliftonia*, *Dalmanella*, *Dolerorthis*, *Eospirigerina*, *Eostropheodonta*, *Fardenia*, *Hindella*, *Leptaena*, *Brevilamnulella*, *Eodictyonella*, *Homoeospira*, *Leptoskelidion*, *Mendacella*, *Orthostrophella*, *Stegerhynchus*, *Thebesia* (Amsden, 1974).

E2, Bryant Knob Formation, USA: *Dalmanella*, *Dolerorthis*, *Eospirigerina*, *Fardenia*, *Hindella*, *Leptaena*, *Platystrophia*, *Brevilamnulella*, *'Diceromyonia'*, *Homoeospira*, *Mendacella*, *Stegerhynchus*, *Thebesia* (Amsden, 1974).

E3, Leemon Formation, Missouri, USA: *Cliftonia*, *Dalmanella*, *Dolerorthis*, *Eospirigerina*, *Fardenia*, *Hindella*, *Leptaena*, *Biparetis*, *Brevilamnulella*, *Stegerhynchus*, *Strophomena*, *Thaerodonta*, *Thebesia*, *Whitfieldella* (Amsden, 1974).

E4, Keel Formation, Oklahoma, USA: *Dalmanella*, *Dolerorthis*, *Hindella*, *Leptaena*, *Brevilamnulella*, *Eodictyonella*, *Leptoskelidion*, *Orthostrophella*, *Stegerhynchus* (Amsden, 1974).

E5, Mosalem Formation, Iowa, USA: *Dalmanella*, *Eospirigerina*, *Fardenia*, *Eostrophonella*, *Platystrophia*, *Leptaena*, *Dolerorthis*, *Whitfieldella*, *Mendacella*, *Eoplectodonta* (Stott and Jin, 2007).

E6, Manitoulin Formation, Southern Ontario, Canada: *Hesperorthis*, *Platystrophia*, *Dalmanella*, *Mendacella*, *Fardenia*, *Furcitella*, *Leptaena*, *Stegerhynchus*, *Thebesia*, *Orthorhynchillion*, *Zygospiraella*, *Sypharatrypa*, *Eospirigerina*, *Hindella* (=their *Cryptothyrella*), *Whitfieldella*, *Rhynchotreta* (Stott and Jin, 2007).

E7, Laframboise Member of Ellis Bay Formation, Anticosti, E Canada: *Eochonetes*, *Eodictyonella*, *Eoplectodonta*, *Eostrophonella*, *Fardenia*, *Furcitella*, *Hindella*, *Hirnantia*, *Leptaena*, *Mendacella*, *Vinlandostrophia* (Dewing, 1999; Jin and Zhan, 2008; Copper *et al*., 2013; Copper and Jin, 2014).

E8, SW Mackenzie, W Canada: *Dalmanella*, *Eospirigerina*, *Epitomyonia*, *Platystrophia*, *Brevilamnulella*, *Kozlowskiaphomena* (Jin and Chatterton, 1997).

E9, Upper Tirekhtyakh Formation (Q 107-4/4), Mirny Creek, Kolyma: *Biparetis*, *Brevilamnulella*, *Cliftonia*, *Dalmanella*, *Dolerorthis*, *Eoplectodonta*, *Eospirigerina*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hesperorthis*, *Hindella*, *Hyattidina*, *Isorthis*, *Leptaena*, *Protanastrophia* (=their *Parastrophinella*, see Jin and Popov, 2008), *Plectatrypa*, *Stegerhynchus*, *Thebesia*, *Triplesia* (Koren *et al*., 1983; Koren and Sobolevskaya, 2008). Note that *Hirnantia*?, *Rhynchotrema*?, *Plectothyrella*?, and *Dorytreta*? are not included in this list.

E10, Upper Tirekhtyakh Formation (Q 107-5/6, 8), Mirny Creek, Kolyma: *Biparetis*, *Dalmanella*, *Eoplectodonta*, *Eospirigerina*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hindella*, *Leptaena*, *Thebesia* (Koren *et al*., 1983; Koren and Sobolevskaya, 2008).

E11, Upper Tirekhtyakh Formation (7-3), Neznakomk Creek, Kolyma: *Brevilamnulella*, *Dalmanella*, *Eoplectodonta*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hindella*, *Leptaena*, *Protanastrophia* (=their *Parastrophinella*, Jin and Popov, 2008) (Koren *et al.*, 1983; Koren and Sobolevskaya, 2008).

E12, Upper Tirekhtyakh Formation (7-4), Neznakomk Creek, Kolyma: *Brevilamnulella*, *Dalmanella*, *Dolerorthis*, *Eoplectodonta*, *Eospirigerina*, *Eostropheodonta*, *Fardenia*, *Giraldibella*, *Hindella*, *Leptaena*, *Plectatrypa*, *Protanastrophia* (=their *Parastrophinella*, Jin and Popov, 2008), *Stegerhynchus* (Koren *et al.*, 1983; Koren and Sobolevskaya, 2008). Note that *Plectothyrella*? is not included in the list.

E13, Upper Tirekhtyakh Formation, Mirny Creek (107-1 and 2), Kolyma: *Eoplectodonta*, *Eostropheodonta*, *Leptaena*, *Thebesia* (belonging to *M. extraordinarius* Biozne) (Koren *et al.*, 1983; Koren and Sobolevskaya, 2008).

E14, Upper part of Tirekhtyakh Formation, Neznakomk Creek (7-2a), Kolyma: *Biparetis*, *Cliftonia*, *Dalmanella*, *Eostropheodonta*, *Eoplectodonta*, *Eospirigerina*, *Fardenia*, *Giraldibella*, *Hindella*, *Leptaena*, *Protanastrophia* (=their *Parastrophinella*, see Jin and Popov, 2008), *Triplesia* (belonging to *M. extraordinarius* Biozne) (Koren *et al.*, 1983; Koren and Sobolevskaya, 2008).

E15, Top part of Langøyene Formation, Oslo-Asker Region, Norway: *Hindella*, *Rostricellula*, *Brevilamnulella*, *Eostrophonella*, *Leptoskelidion*, *Thebesia* (Cocks, 1982; this paper).

E16, *Thebesia* Association, at Hovedoya S 10, Oslo-Asker Region, Norway: *Thebesia*, *Hindella*, *Leptoskelidion* (Cocks, 1982; Brenchley and Cocks, 1982). Note that *Comatopoma*? is not included in the list.

E17, *Brevilamnulella* Association, top portion of Langåra Formation, Oslo-Asker Region, Norway: *Brevilamnulella*, *Rostricellula* (Cocks, 1982; Brenchley and Cocks, 1982)

E18, Klinkenberg Formation, Hadeland, Oslo-Asker Region, Norway: *Askerina*, *Dalmanella*, *Fardenia*, *Leptaena*, *Zygospiraella* (Heath and Owen, 1991; Baarli, 2019)

E19, Loka Formation, Östergötland, Sweden: *Cliftonia*, *Dalmanella*, *Epitomyonia*, *Fardenia*, *Hindella*, *Leptaena*, *Alispira*, *Stegerhynchus* (Bergström and Bergström, 1996; Rong *et al.*, 2008b; Jin *et al.*, 2010; this paper).

E20, Dorozhnin Formation, Gornyi Altai: *Alispira*?, *Brevilamnulella*, *Cliftonia*, *Dedzetina*, *Eospirigerina*, *Eostropheodonta*, *Epitomyonia*, *Kinnella*?, *Leangella*, *Leptaena*, *Rostricellula*, *Stegerhynchus*, *Streptis*, *Giraldibella*, *Zygospiraella*? (Kulkov and Severgina, 1987)

E21, Upper Ashgill rocks, Dzhindy-Dariya, Zeravshano-Gissar Mountains, Central Asia: *Eospirigerina*, *Brevilamnulella*, *Djindella*, *Koigia*, *Parastrophina*, *Thebesia*, *Whitfieldella* (Menakova, 1991).

E22, Basal Anji Formation (AFL 159), Dakengwu, Chun'an, Zhejiang, S China: *Eoplectodonta*, *Eospirigerina*, *Glyptorthis*, *Levenea*, *Leptaena*, *Rostricellula*, *Brevilamnulella*, *Cathaysiorthis*, *Eospirifer*, *Hesperorthis*, *Mendacella*, *Plectorthis*, *Sulcatospira*, *Thebesia*, *Whitfieldella* (Rong *et al.*, 2013).

E23, Basal Anji Formation (AFL 161), Dakengwu, Chun'an, Zhejiang, S China: *Eopholidostrophia*, *Eoplectodonta*, *Eospirigerina*, *Epitomyonia*, *Fardenia*, *Glyptorthis*, *Hindella*, *Levenea*, *Leptaena*, *Paracraniops* (=their *Craniops*), *Skenidioides*, *Salopina*, *Triplesia*, *Alispira*, *Brevilamnulella*, *Cathaysiorthis*, *Hesperorthis*, *Katastrophomena*, *Kiaeromena*, *Mendacella*, *Plectorthis*, *Sulcatospira*, *Thebesia*, *Xenocrania* (Rong *et al.*, 2013).

E24, Yankou Formation (AFL 295), Shizishan, Yuhang, Zhejiang, S China: *Dolerorthis*, *Eospirigerina*, *Epitomyonia*, *Fardenia*, *Glyptorthis*, *Levenea*, *Leptaena*, *Cathaysiorthis*, *Chunanella*, *Eospirifer*, *Sulcatospira*, *Xenocrania* (Rong *et al.*, 2013).

E25, Yankou Formation (AFL 296–299), Shizishan, Yuhang, Zhejiang, S China: *Aegiromena*, *Anisopleurella*, *Dolerorthis*, *Eoplectodonta*, *Eospirigerina*, *Eostropheodonta*, *Epitomyonia*, *Glyptorthis*, *Leangella*, *Paracraniops* (=their *Craniops*), *Skenidioides*, *Salopina*, *Chunanella*, *Pseudocrania*, *Sulcatospira*, *Yuhangella* (Rong *et al.*, 2013).

E26, Yankou Formation (AFL 303), Shizishan, Yuhang, Zhejiang, S China: *Aegiromena*, *Anisopleurella*, *Dolerorthis*, *Eoplectodonta*, *Eospirigerina*, *Epitomyonia*, *Glyptorthis*, *Leangella*, *Paracraniops* (=their *Craniops*), *Skenidioides*, *Salopina*, *Templeella*, *Brevilamnulella*, *Eospirifer*, *Mendacella*, *Pseudocrania*, *Sulcatospira*, *Xenocrania*, *Yuhangella* (Rong *et al.*, 2008a).

E27, Basal Anji Formation (Bed 44: AEP 708-8), Tangjia, Lin'an, Zhejiang, S China: *Brevilamnulella*, *Eoplectodonta*, *Eospirigerina*, *Fardenia*, *Glyptorthis*, *Levenea*, *Leptaena*, *Mendacella*, *Paracraniops*, *Sulcatospira*, *Triplesia* (Overlying the brachiopods–bearing beds, there occur graptolites indicative of lower *M. extraordinarius* Biozone) (Zhang *et al.*, 2007; Rong *et al.*, 2013).

E28, Basal part of Anji Formation (Bed 17: AEP728), Ximenshan-Tangwuli, Deqing, northwestern Zhejiang, SE China: *Aegiromena* (Zhang *et al*., 2007).

E29, Shiqian Bed, Zhaojiawan, Shiqian, northeastern Guizhou, S China: *Cathaysiorthis* (Hu *et al*., 1983; this paper).

E30, South Africa: *Arenorthis*, *Eostropheodonta*, *Orbiculoidea*, *Plectothyrella*, *Trematis*, *Kosoidea*, *Palaeoglossa* (Cocks *et al*., 1970; Bassett *et al*., 2009).

Appendix II

This is the detail caption for the *Hirnantia* Fauna–bearing localities shown in the Figure 2. I. Basin: I_1 north of the northern margin of the Yangtze Region, I_2 Central Hunan basin; largely black graptolitic siliciclastic facies. II. Slope and depression: deep water shelly assemblages; white circle (50–72): e.g., the *Paromalomena–Aegiromena* Association (BA 4) and *Aegiromena* Association (BA 5). III. Platform: Upper Yangtze Region, rich in brachiopods and trilobites (BA 2–BA 3); yellow circle (1–15): mostly limestone intercalated with argillaceous limestone yielding the *Dalmanella–Plectothyrella* Community (upper BA 2), associated with rugose corals; brown circle (16–42): various brachiopod associations with moderate diversity (lower BA 2 to upper BA 3); purple circle (43–49): the *Hirnantia* Fauna with a higher diversity (usually lower BA 3). Grey square: the Hirnantian rocks are missing and no *Hirnantia* Fauna–bearing beds are developed. For example, the Xiang (Hunan)–E–Xi (western Hubei) Uplift has commonly described as an underwater highland during the Hirnantian. Alternatively, it is inferred that the Kuanyinchiao Bed may have been deposited there, but was eroded away afterwards due to the later uplift on the evidence from community analysis of brachiopods. IV. Supposedly near-shore area along northern margin of the Cathaysian Land with large amounts of clastic deposits; coarse grained, and very few fossils; yellow square (73–77): the lower–middle

Hirnantian shallow water deposits, mainly greyish green sandstone and siltstone, intercalated with mudstone, i.e., the Wenchang Formation, yielding brachiopods dominated by *Rhynchotrema* and sometimes by gastropods (very low diversity and high abundance, BA 2); red pentagon (78–81): marine red beds, i.e., the Hongjiawu Formation, a series of purple red, yellow and grey sandstones, siltstones and mudstones, lacking macrofossils (BA 1). V. Qinling–Dabie Orogenic Belt.

Abbreviations of provinces: A-Anhui, C-Chongqing, G-Guizhou, HB-Hubei, HN-Hunan, JX-Jiangxi, JS-Jiangsu, S-Sichuan, SH-Shaanxi, Y-Yunnan, and Z-Zhejiang. 1. Qianjin, Ganluo (S); 2. Langzhu, Butuo (S); 3. Huanggexi, Daguan (Y); 4. Heitupo, Linkou, 5 and 6. Zhonggou west and east, Yanzikou, north of Bijie (G); 7. Yangliugou and 8. Shichang, Renhuai (G); 9. Daijiagou, Tongzi (G); 10. Baixiangyan, Zunyi (G); 11. Dongkala, Fenggang (G), 12. Longjingpo, Wuchuan (G); 13. Heshui, Yinjiang (G); 14. Ludiping, Songtao (G); 15. Wenyuan drill (S); 16. Jiaodingshan, Hanyuan (S); 17. Wanhe, Yongshan (Y); 18. North of Yanjin (Y); 19. Feilong, Fushun (S); 20. Rongchang (C); 21. Puxing, Xuyong (S); 22. Yinshuiwan, Xishui (G); 23. Zhicaogou, Renhuai (G); 24. Guanyinqiao, Qijiang (C); 25. Hanjiadian and 26. Honghuayuan, Tongzi (G); 27. Jiadanwan, Zunyi (G); 28. Balixi, Fenggang (G); 29. North of Zheng'an (G); 30. Bayu, Daozhen (G); 31. Wanzu, Pengshui (C); 32. Ganxi, Yanhe (G); 33 and 34. Datianba and Miaoquan, Xiushan (C); 35 and 36. Huatian and Cangling, Youyang (C, provided by Ge Xiangying and identified by the present author); 37. Shaba and 38. Lishui, Qianjiang (C); 39. Maoba, Lichuan (HB); 40. Qiliao, Shizhu (C); 41. Dalianghui, Wangcang (S); 42. Guabaoyan, Nanzheng (SH); 43. Qiaoting, Nanjiang (S); 44. Shuanghe, Changning (S); 45. Huangtian, Gongxian (S); 46. Gusong, Xingwen (S); 47, 48 and 49. Huanghuachang, Wangjiawan and Tangya, north of Yichang (HB); 50. Liangshan, Nanzheng (SH); 51. Xiaoxingliangzi, Zhenba (SH); 52. Miaoba, Chengkou (C); 53. Muchanggou, Shizhu (C); 54. Tianba and 55. Wenfeng, Wuxi (C); 56. Jiuhu,

Shennongjia (HB); 57. Lianghekou, Badong (HB); 58. Maqiao, Baokang (HB); 59. Daheba, Zhangjiajie (HN); 60. Jinglongqiao, Cili (HN); 61. Baimaquan, Taoyuan (HN); 62. Guantangyuan, Wuning (JX); 63. Taokeng, Taiping (A); 64. Bagongli, Jingxian (A); 65. Jurong, Zhenjiang (JS); 66. Sanqiaobu, Deqing (Z); 67. Huangshu, Anji (Z); 68. Xiaofeng, Anji (Z); 69. Anle, Yuhang (Z); 70. Shangluojia, Lin'an (Z); 71. Yankou, Yuqian (Z); 72. Tantou, Chun'an (Z); 73. Gaotingshan, Hangzhou (Z); 74. Laojiaoshan, Hangzhou (Z); 75. Wenchang, Chun'an (Z); 76. Xutangwu, Jiande (Z); 77. Dakengwu, Chun'an (Z); 78. Tongjia and Zhoutang, Changshan (Z); 79. Hongjiawu, Daqiao, Jiangshan (Z); 80. Shiyang, Jiangshan (Z); 81. Wangjiaba, Yushan (JX). (Paleogeographic reconstruction based on Rong *et al*., 2010, 2018; Liu *et al*., 2012)

Appendix III

The following eleven most common genera in the *Hirnantia* Fauna have many of their own predominant occurrences in communities or associations, indicating that they may have had more optimum habitats than the others during the end Ordovician mass extinction.

1. Hirnantia (17 examples, 5 geographic units): 47.2% of the whole assemblage at the localities 109 (Rambergøya 7, Oslo), Norway (Brenchley and Cocks, 1982); 41% in a representative of the *Hirnantia* Asspciation in Oslo-Asker Region (Brencley and Cullen, 1984); 16.1% of a relatively higher diversity sample at the locality 2, Västergötland, Sweden (Bergström, 1968) (Baltica). 42% of a median diversity assemblage at Qijiang, 34.8% and 29.1% of two higher diversity samples (AXU 454 and 455) at Miaoquan, Xiushan, southern Chongqing; 38% and 34.9% at Jiancaohe, Zunyi and Tiancheng, Meitan, 32% at Hanjiadian, Tongzi, northern Guizhou (Rong, 1986; Huang *et al.*, 2020); 27.1% at Qiaoting, Nanjiang, northern Sichuan; 21.9 and 21.7% of a high diversity

Hirnantia fauna at Chaqi and Wangjiawan, Yichang, western Hubei (South China). 38.2% and 32.5% at Zhiwazuogu (ADG 46 and 47), at Yongzhu, Xainza, central Xizang; 26.4% at Xainza, Xizang (Rong and Xu, 1987) (Lhasa). 29.3% in the sample YMS-01b at Mangjiu, Mangshi, western Yunnan (Huang *et al.*, 2020c) (Sibumasu). The most abundant genus in the *Hirnantia* Fauna at San Juan, Argentina (Benedetto, 1986) (Pre–Cordillera)

2. *Dalmanella* (15 examples, 5 units): 66.7% of the lower diversity brachiopods in the samples at Yanzikou, Bijie and Shichang, Renhuai (Rong and Li, 1999), 56.7% and 48.7% of the whole fauna at Huangban and Ludiping, Songtao, 45.1% and 34.3% at Liangfengya, Tongzi and 38.7% at Zheng'an, northern Guizhou (this paper); 42.2% and 36.7% in the samples (Nos. AFN 3048 and 3047) at Shuanghe, Changning, southern Sichuan (Li *et al.*, 2009); 39.0% and 24.8% at Datianba and Miaoquan (AXU 453), Xiushan, southern Chongqing; (South China). 81% in Oslo-Asker Region, Norway (Brencley and Cullen, 1984); 37% in Estonia and Latvia (Hints and Harper, 2015) (Baltica). 34.9% in Chu–Ili (Nikitin *et al.*, 1980) (Kazakhstan). 31.8% at Mencher-Pudding Stone, Maine (D), USA (this paper) (Avalonia). Several hundred specimens, the most abundant species in a high diversity *Hirnantia* fauna at Bechovice and Nova Ves, Bohemia (Marek and Havlíček, 1967) (Perunica).

3. *Kinnella* (10 examples, 7 units): 52.2% of the *Hirnantia* brachiopod association at Stawy, Southern Poland (Temple, 1965) (Baltica). 36.4% in the brachiopod sample (No. 3047) at Shuanghe, Changning, southern Sichuan (Li *et al.*, 2009); 33.5% at Tongguyuan, Tongzi, northern Guizhou; 22% at Yichang, western Hubei (Rong, 1984; Wang *et al.*, 1987) (South China). 38.5% at Pond Pitch-Haskell Rock, Maine (C), USA (this paper); 31.6% at Hol Beck, Westmorland, England (Temple, 1965) (Avalonia). 22.6% in Mandalay Division, Myanmar (Rong *et al.*, 2020)

(Sibumasu). Several hundred specimens in Bohemia (Marek and Havlíček, 1967) (Perunica). Very abundant in southern France (Álvaro *et al.*, 2016) (European peri‐Gondwana).

4. *Eostropheodonta* (10 examples, 4 units): 48.6% of a low diversity fauna at the locality 1, Västergötland, Sweden (Bergström, 1968) (Baltica). 46.4% of a moderate diversity *Hirnantia* fauna at Donggongsi, Zunyi, 30.8% of a lower diversity *Hirnantia* fauna at Dongkala, Fenggang, 37% of a moderate diversity of the fauna at Hanjiadian, Tongzi (this paper), northern Guizhou; 37% at Guanyinqiao, Qijiang, southern Chongqing (Wang *et al.*, 1957) (South China). 41.4% of the whole brachiopods at the locality H1 in High Mains Formation of Girvan, Scotland (Harper, 1981) (Laurentia). 40.8% at Cautley district, England (Ingham, 1966); 40.2% at Kildare, Ireland (Ingham, 1966); more than 30% at Hirnant Quarry Bala, North Wales (Temple, 1965; Cocks and Price, 1975; Brenchley and Cullen, 1984) (Avalonia).

5. *Aegiromena* (8 examples, 3 units): 100% of the whole brachiopod association at Liangbei Road, Zhenba, southern Shaanxi (this paper); 100% and 92.3% at Baimaquan, Taoyuan, and Jinglongqiao, Cili, northern Hunan (Rong *et al.*, 2019); 66.7% of the whole brachiopods in a low diversity association of the deep water *Hirnantia* Fauna at Beigong, Jingxian, Anhui; 26.7% of the AFN 3050 in the top of the Kuanyinchiao Bed at Shuanghe, Changning, southern Sichuan (Li *et al.*, 2009); the most common genus in a deeper water association at Qiliao, Shizhu, southern Chongqing (this paper) (South China). 79% in a deeper water association at Santun, Thailand (Cocks and Fortey, 1997) (Sibumasu). A single brachiopod taxon in a deep water association at Nifsåsen, Jämtland, central Sweden (Dahlqvist *et al.*, 2010) (Baltica).

6. *Hindella* (8 examples, 3 units): 68.7% and 41.4% of the whole fauna at the localities H2 and H1 in High Mains Formation of Girvan, Scotland (Harper, 1981) (Laurentia). 35% of a further *Hirnantia*

fauna at Kildare Limestone, Ireland (Cocks and Price, 1975), 34.5% at the Locality 13030, Maine (A), USA (this paper); the most abundant taxon of the whole brachiopods in the Graig-wen Sandstone, Meifod (20.3%) and Llanfyllin (25.1%), Wales (Brenchley *et al.*, 2006; Brenchley and Cullen, 1984) (Avalonia). 41.4% and 40% in the *Hindella–Cliftonia* association at the Locality 33 (Langåra W17, Norway) and 30 (Konglungen E16, Norway) (Brenchley and Cocks, 1982) (Baltica).

7. Cliftonia (8 examples, 3 units): 68.8%, 64% and 47.2% of the whole assemblage at the localities 9 (Langara W17, Asker), Langara west (Asker), and 107 (Ranbergøya 7, Oslo) respectively, Norway (Brenchley and Cocks, 1982); 40% in the *Hindella–Cliftonia* association at the Locality 30 (Konglungen E16, Norway) (Brenchley and Cocks, 1982); 32% in a sample of the *Hindella/Cliftonia* Association (Brenchley and Cullen, 1984); 26.7% of a moderate diversity fauna at the Locality 13, Västergötland, Sweden (Bergström, 1968) (Baltica). 42.1% of a sample (AFF 295) of the Kuanyinchiao Bed at Hanghuayuan, Tongzi, northern Guizhou (South China). 36.7% at Kildare, Ireland (Wright, 1968) (Avalonia).

8. Plectothyrella (6 examples, 3 units): 51% of the whole fauna at Jiaodingshan, Hanyuan, western Sichuan (Feng *et al.*, 1991) (South China). 44.5% at Percé, Québec, East Canada (Lespérance and Sheehan, 1976) (Laurentia). 30.6% and 16.1% at the Localities 8 and 2, Västergötland, Sweden (Bergström, 1968) (Baltica). 20% at Locality No. 13031, Maine (B), USA (this paper) (Avalonia). Predominant in the Ribeira do Bracal Formation (Hirnantian) at the Locality 3 in Central Portugal (Colmenar *et al.*, 2018) (European peri‐Gondwana).

9. Fardenia (2 examples, 2 units): 43% of a relatively higher diversity assemblage at the locality 5, Västergötland, Sweden (Bergström, 1968) (Baltica). 38.3% and 29.3% in the samples YMS-01

and 01b at Mangjiu, Mangshi, western Yunnan (Huang *et al.*, 2020c) (Sibumasu).

10. Paromalomena (2 examples, 2 units): 28.0% of the whole fauna (ADG 24) at 15 km, south of Yongzhu Bridge, Xainza County, central Xizang (Rong and Xu, 1987) (Lhasa); 20.9% at Berwyns, North Wales (Brenchley and Cullen, 1984). In addition, there are several examples in which *Paromalomena* is the second or third most common genus in relatively higher diversity *Hirnantia* Fauna at Ludiping and Huangban, Songtao, norther Guizhou (18.6% and 16.3%) (This paper), Mandalay, Myanmar (13.8%) (Rong *et al.*, 2020), and 17.2% at Wangjiawan, Yichang, western Hubei (Wang *et al.*, 1987).

11. Leptaena (1 example, 1 unit): the most common genus known in the Hirnantian rocks of Southern Island, New Zealand (Cocks and Cooper, 2004).

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